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IRON-MANGANESE INTERRELATIONSHIPS IN PLANT NUTRITION[1]

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The results of various workers concerning the relationships between iron and manganese in plant nutrition are apparently conflicting. Johnson (8) obtained complete recovery from iron deficiency when a solution of ferrous sulphate was applied to pineapple plants growing on a soil high in manganese; but, when the same solution was applied to the soil, he obtained only partial recovery, or no recovery at all. The degree of recovery was inversely proportional to the amount of manganese present in the soil. Chapman (3) noted that when apple and pear trees were injected with manganese sulphate one year in advance of spraying with an iron solution, the iron deficiency was corrected only in local areas of the leaves. According to Thorne and Wallace (15), spraying manganese-deficient apricot trees with a solution of ferrous sulphate resulted in increased severity of manganese deficiency symptoms.

From their work, Somers, Shive and Gilbert (12, 13, 14) concluded that the optimum ratio of iron to manganese in culture solutions for the growth of soybeans was 2 : 1, and any appreciable departure from this ratio resulted in the appearance of either iron or manganese toxicity symptoms. These workers also claim that symptoms of manganese toxicity correspond to those of iron deficiency and vice versa. Hopkins and his co-workers (5) were led to believe that the interaction of iron, manganese, and light is an important determinant controlling the oxidation-reduction potential of green plants. In proper balance, a normal range of the oxidation-reduction potential resulted. When not in proper balance, a too high or too low range of potential for plant tissues occurred, and toxicity appeared. However, they obtained normal growth of plants in culture solutions with iron-manganese ratios much wider than 2 : 1, and found no toxicity from iron, regardless of the ratio. The optimum iron-manganese ratio of the culture solutions in which Morris and Pierre (10, 11) grew lespedeza was 10 : 1. No evidence was found to support Somers and Shive's theory that a rather definite iron-manganese ratio is necessary for normal growth. Moreover, they observed that iron deficiency symptoms of lespedeza are not identical with manganese toxicity symptoms.

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In view of such conflicting results present in the literature, solution culture tests were conducted in the greenhouse to study the effect of various concentrations of iron and manganese and various ratios of these two elements in the substrate on the growth of plants and the development of nutritional symptoms. The soybean was chosen as the indicator plant because it is reported (2) that this plant requires medium amounts of manganese and iron. A description of the experimental procedure follows.

EXPERIMENTAL PROCEDURE

Seeds of soybeans, Hawkeye variety, were sprouted in quartz sand. When the seedlings were approximately two inches in height, the cotyledons were removed and the seedlings transferred to complete nutrient solutions containing 18 p.p.m. of phosphorus and variable amounts of iron and manganese. Manganese was supplied as manganese chloride and iron as ferric citrate.

Three different tests were carried on. The first was designed to study the effect of various concentrations of manganese on the growth of soybeans. Manganese concentrations of 0.01, 0.1, 1.0, 2.5, 5.0, 7.5, 10.0 and 12.5 p.p.m. were used in combination with 5.0 and 15.0 p.p.m. The second test was designed to study the effect of various concentrations of iron on the growth of soybeans. Iron concentrations in the nutrient solutions of 2.5, 5.0, 10.0, 15.0, 20.0 and 25.0 p.p.m. were used in combination with 0.1 and 1.0 p.p.m. of manganese. Finally, the third test was designed to study the effect of two ratios, one narrow and the other wide, of iron to manganese in solution on the growth of soybeans. Various amounts of manganese and iron were added to the basic solution, so that six solutions had a ratio of iron to manganese of 2 : 1 and six solutions a ratio of 30 : 1.

In all three sets, the pH of the solutions was maintained at approximately 4.7 with addition of either H_2SO_4 or NaOH, in accordance with requirements. The concentration of phosphorus in solution was kept at the low level of 18 p.p.m. to avoid removal of any appreciable amount of iron from the solution by precipitation. It was found in a preliminary trial that 1.12 times the calculated amount of ferric citrate would approximately compensate for the amount of iron precipitated in the nutrient solutions at pH 4.7 and containing 18 p.p.m. of phosphorus.

The solutions were renewed twice a week during the early growth period, and every other day during the time when growth was most rapid. This frequent renewal of nutrient solution made possible the maintenance of the iron and manganese concentrations at very nearly the same level throughout the course of the experiment. The solutions were continuously aerated, and water losses by transpiration and evaporation made up twice daily by adding distilled water. Treatments were replicated three times and the jars randomized at weekly intervals as regards location in the greenhouse.

The plants were harvested nine weeks after having been transferred from the quartz sand to the nutrient solutions, dried for 72 hours at 70° C., and then ground in a Wiley mill. For the determination of iron and manganese, a two-gram sample of the ground tissue was subjected to dry ashing at 450° C. for 12 hours. The ash was then taken up in 6N hydro-

TABLE 1.—YIELD AND MANGANESE AND IRON CONTENT OF SOYBEANS (TOPS) GROWN IN NUTRIENT SOLUTIONS CONTAINING VARYING AMOUNTS OF MANGANESE ASSOCIATED WITH TWO LEVELS OF IRON

p.p.m. of Mn in solution	5 p.p.m. Fe in solution				15 p.p.m. Fe in solution			
	Ratio Fe-Mn in solution	Yield in dry weight, gm./jar	p.p.m. in tissue		Ratio Fe-Mn in solution	Yield in dry weight, gm./jar	p.p.m. in tissue	
			Fe	Mn			Fe	Mn
0.01	500 : 1	8.3	158	68	1500 : 1	9.1	268	54
0.1	50 : 1	19.4	139	120	150 : 1	19.5	235	132
1.0	5 : 1	26.8	134	269	15 : 1	33.6	257	189
2.5	2 : 1	25.9	110	341	6 : 1	33.0	204	334
5.0	1 : 1	24.2	116	496	3 : 1	29.6	160	428
7.5	0.66 : 1	17.5	97	602	2 : 1	25.2	171	621
10.0	0.50 : 1	9.4	90	589	1.5 : 1	20.0	139	781
12.5	0.40 : 1	5.2	94	870	1.2 : 1	14.5	122	1006

TABLE 2.—INFLUENCE OF VARIOUS CONCENTRATIONS OF MANGANESE ON THE OCCURRENCE OF IRON AND MANGANESE TOXICITY AND DEFICIENCY IN SOYBEANS

p.p.m. of Mn in solution	5 p.p.m. Fe in solution			15 p.p.m. Fe in solution		
	Ratio Fe-Mn in solution	Pathological symptoms		Ratio Fe-Mn in solution	Pathological symptoms	
		Fe	Mn		Fe	Mn
0.01	500 : 1	Normal	Medium deficiency	1500 : 1	Normal	Severe deficiency
0.1	50 : 1	Normal	Normal	150 : 1	Normal	Slight deficiency
1.0	5 : 1	Normal	Normal	15 : 1	Normal	Normal
2.5	2 : 1	Normal	Very slight toxicity	6 : 1	Normal	Normal
5.0	1 : 1	Normal	Slight toxicity	3 : 1	Normal	Very slight toxicity
7.5	0.66 : 1	Slight deficiency	Medium toxicity	2 : 1	Normal	Slight toxicity
10.0	0.50 : 1	Slight deficiency	Medium toxicity	1.5 : 1	Normal	Medium toxicity
12.5	0.40 : 1	Medium deficiency	Severe toxicity	1.2 : 1	Normal	Severe toxicity

chloric acid, and aliquots of the resulting solution analysed for the two elements. Manganese was determined colorimetrically, following oxidation to permanganate with potassium periodate (9, 16). Iron was also determined colorimetrically after reduction to the ferrous state with hydroxylamine, and formation of an orange-coloured ferrous complex with o-phenanthroline (1, 6, 7).

RESULTS

Yield and chemical analysis data on the dry weight basis, and nutritional symptoms of soybeans (tops) harvested from the three sets mentioned above are presented in Tables 1 to 6. The following scale is used in those tables to characterize the degree of severity of the nutritional symptoms observed on soybean plants:

Expression used	Number of leaves affected in per cent
Very slight	Less than 10
Slight	10 to 25
Medium	25 to 50
Severe	More than 50

Table 3.—Yield and manganese and iron content of soybeans (tops) grown in nutrient solutions containing varying amounts of iron associated with two levels of manganese

p.p.m. of Fe in solution	0.1 p.p.m. Mn in solution				1.0 p.p.m. Mn in solution			
	Ratio Fe-Mn in solution	Yield in dry weight, gm./jar	p.p.m. in tissue		Ratio Fe-Mn in solution	Yield in dry weight, gm./jar	p.p.m. in tissue	
			Fe	Mn			Fe	Mn
2.5	25 : 1	19.8	106	125	2.5 : 1	20.1	99	246
5.0	50 : 1	20.4	128	131	5.0 : 1	25.2	156	207*
10.0	100 : 1	22.0	202	136	10.0 : 1	27.5	211	271
15.0	150 : 1	17.2	240	130	15.0 : 1	34.7	250	276
20.0	200 : 1	12.0	298	140	20.0 : 1	36.5	274	295
25.0	250 : 1	10.2	321	143	25.0 : 1	36.1	307	338

* One of the two replicates contained only 159 p.p.m.

Table 4.—Influence of various concentrations of iron on the occurrence of iron and manganese toxicity and deficiency in soybeans

p.p.m. of Fe in solution	0.1 p.p.m. Mn in solution			1.0 p.p.m. Mn in solution		
	Ratio Fe-Mn in solution	Pathological symtoms		Ratio Fe-Mn in solution	Pathological symptoms	
		Fe	Mn		Fe	Mn
2.5	25 : 1	Normal	Normal	2.5 : 1	Slight deficiency	Normal
5.0	50 : 1	Normal	Normal	5.0 : 1	Normal	Normal
10.0	100 : 1	Normal	Normal	10.0 : 1	Normal	Normal
15.0	150 : 1	Normal	Slight deficiency	15.0 : 1	Normal	Normal
20.0	200 : 1	Normal	Medium deficiency	20.0 : 1	Normal	Normal
25.0	250 : 1	Normal	Medium deficiency	25.0 : 1	Normal	Normal

Increasing the amount of soluble manganese in the nutrient solution from 0.01 to 1.0 p.p.m. resulted in greatly increased yields, whereas decreases in yield were experienced with more than 1.0 p.p.m. (Table 1). However, no manganese toxicity symptoms were observed with less than 2.5 p.p.m. of soluble manganese when the iron concentration was 5.0 p.p.m., and less than 5.0 p.p.m. when the iron concentration was 15.0 p.p.m. (Table 2). Also, plants growing in 0.1 p.p.m. of manganese and 15.0 p.p.m. of iron in the nutrient solution showed manganese deficiency symptoms, whereas plants growing in 0.1 p.p.m. of manganese and 5.0 p.p.m. of iron were normal (Table 2). Thus, an increase in the iron concentration in the substrate appears to be effective in reducing manganese toxicity and increasing manganese deficiency.

Increasing the amount of soluble iron in the nutrient solution from 2.5 to 20.0 p.p.m., resulted in greatly increased yields (Table 3). With 25.0 (Table 3) and 30.0 (Table 5) p.p.m. of iron, the yields had a tendency to level off, indicating that the plants were getting sufficient iron at this concentration. Slight iron deficiency was observed on plants growing in nutrient solutions containing 2.5 p.p.m. of iron and 1.0 p.p.m. of manganese, whereas normal growth was obtained from plants growing in nutrient

TABLE 5.—YIELD AND MANGANESE AND IRON CONTENT OF SOYBEANS (TOPS) GROWN IN NUTRIENT SOLUTIONS IN WHICH TWO RATIOS, ONE NARROW AND THE OTHER WIDE, OF IRON TO MANGANESE WERE MAINTAINED

Fe-Mn ratio 2 : 1 in solution					Fe-Mn ratio 30 : 1 in solution				
p.p.m. in solution		Yield in dry weight, gm./jar	p.p.m. in tissue		p.p.m. in solution		Yield in dry weight, gm./jar	p.p.m. in tissue	
Fe	Mn		Fe	Mn	Fe	Mn		Fe	Mn
0.2	0.1	6.7	52	118	0.3	0.01	4.9	59	60
1.0	0.5	12.0	74	183	3.0	0.10	19.0	161	147
2.0	1.0	16.9	92	260	7.5	0.25	28.5	200	347*
5.0	2.5	24.3	127	324	15.0	0.50	35.3	266	225
10.0	5.0	25.7	176	402	30.0	1.0	35.8	332	319
15.0	7.5	20.7	188	685	60.0	2.0	34.2	380	404

* Plants from both replicates were abnormally high in manganese.

TABLE 6.—INFLUENCE OF VARIOUS IRON-MANGANESE RATIOS IN NUTRIENT SOLUTION ON THE OCCURRENCE OF IRON AND MANGANESE TOXICITY AND DEFICIENCY IN SOYBEANS

Fe-Mn ratio 2 : 1 in solution				Fe-Mn ratio 30 : 1 in solution			
p.p.m. in solution		Pathological symptoms		p.p.m. in solution		Pathological symptoms	
Fe	Mn	Fe	Mn	Fe	Mn	Fe	Mn
0.2	0.1	Severe def.	Normal	0.3	0.01	Severe deficiency	Med. deficiency
1.0	0.5	Med. deficiency	Normal	3.0	0.1	Normal	Normal
2.0	1.0	Slight deficiency	Normal	7.5	0.25	Normal	Normal
5.0	2.5	Normal	Very slight toxicity	15.0	0.50	Normal	Normal
10.0	5.0	Normal	Very slight toxicity	30.0	1.0	Normal	Normal
15.0	7.5	Normal	Slight toxicity	60.0	2.0	Normal	Normal

solutions containing 2.5 p.p.m. of iron and 0.1 p.p.m. of manganese (Table 4). Thus, a decrease in the manganese concentration in the substrate appears to be effective in reducing the severity of iron deficiency.

It should be noted that, where the iron-manganese ratio was wider than 150 : 1 (Table 4), manganese deficiency, but not iron toxicity, symptoms occurred; and where the ratio was 2.5 : 1, iron deficiency, but not manganese toxicity, occurred. This is in contrast with Somers' and Shive's finding (14), that manganese deficiency symptoms are necessarily associated with iron toxicity symptoms, and vice versa.

When the iron-manganese ratio was maintained at the 30 : 1 level in the nutrient solution, by using varying concentrations of the two elements (Table 6), iron deficiency and manganese toxicity could be easily avoided. On the contrary, normal growth could not be obtained when the iron-manganese ratio in the nutrient solution was maintained at the 2:1 level by using varying amounts of these two elements (Table 6). Moreover, the fact that the yields (Table 5) ranged from 4.9 grams, with 0.3 p.p.m. of iron and 0.01 p.p.m. of manganese, to 35.3 grams, with 15.0 p.p.m. of iron and 0.5 p.p.m. of manganese in the nutrient solution, indicates that the concentration of the elements iron and manganese in the medium has some importance over and above their ratio.

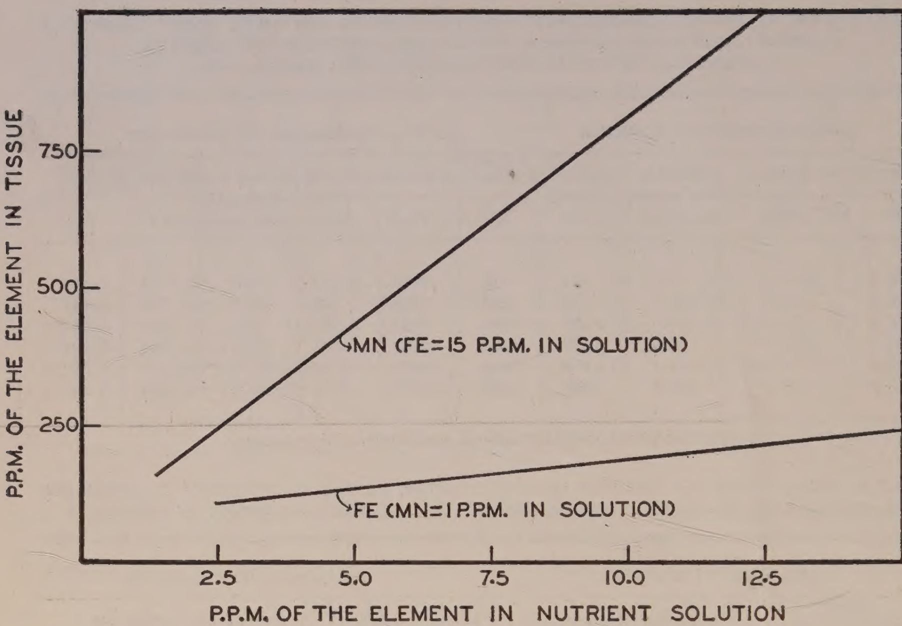

FIGURE 1. Manganese and iron uptake by soybeans (tops) in nutrient solutions containing varying amounts of those two elements.

DISCUSSION

Attention is drawn to the striking difference between iron and manganese as regards absorption by soybean plants (Figure 1). In fact, healthy plants grown in the solutions containing 1.0 p.p.m. of manganese had about 200 p.p.m. of this element in the tops on the dry weight basis, whereas severely injured plants grown in the solutions containing 12.5 p.p.m. had about 1000 p.p.m. The variations in the iron content of the tissue were not so pronounced as those in manganese. As for example, plants growing in the solutions containing 3.0 p.p.m. of iron had about 175 p.p.m. of iron in the tops, whereas plants growing in the nutrient solutions containing 60 p.p.m. had about 375 p.p.m. This differential absorption of iron and manganese by soybeans can be a sound explanation of the sensitivity of this plant to manganese toxicity, as well as of the fact that no iron toxicity was observed.

Hildebrandt, Riker and Duggar (4) found that ferric sulphate inhibited growth of sunflower tissue cultures at concentrations of 20 to 40 p.p.m., and tobacco cultures at 40 p.p.m. They first thought that this inhibition was due to iron toxicity; but, in a further study, they observed that good growth could be obtained if the medium contained 20 to 40 p.p.m. of ferric tartrate in place of ferric sulphate. Thus, they concluded that this effect of ferric sulphate was correlated with increased acidity of the medium and manganese solubility, rather than with the iron concentration itself. In fact, with sunflower cultures, the media with 20 and 40 p.p.m., respectively, of ferric sulphate had final pH values ranging from 4.6 to 4.9 and from 3.7 to 4.3.

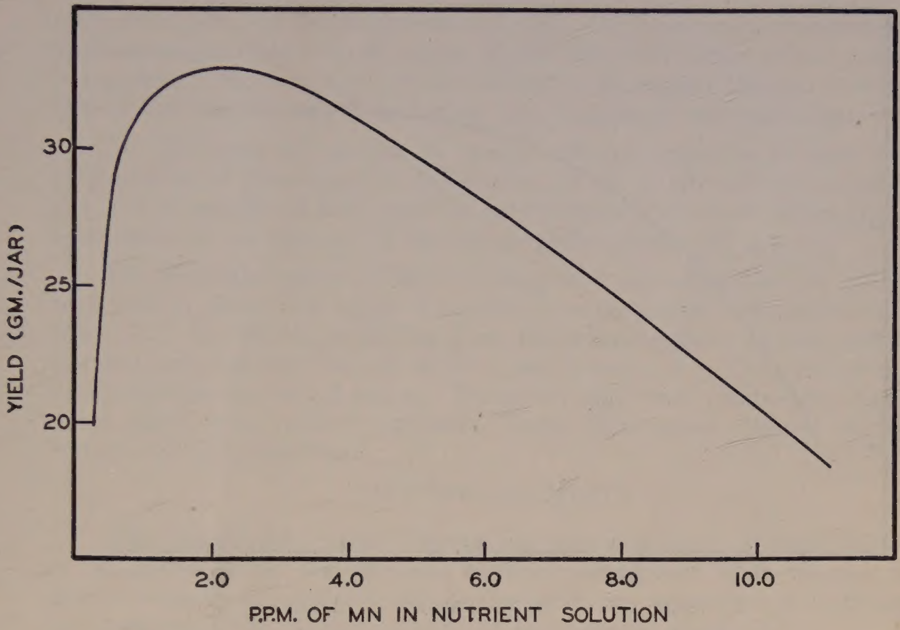

FIGURE 2. Influence of the manganese concentration in the nutrient solution on the yield of soybeans (iron constant at 15 p.p.m. in the nutrient solution).

The response of soybeans to various concentrations of manganese and iron in the nutrient solution is shown graphically in Figures 2 and 3. The curve shown in Figure 2 represents the effect of various concentrations of manganese in the nutrient solution on the yield of soybeans, with the iron concentration constant at 15.0 p.p.m. If both iron and manganese concentrations were variable, a series of curves crossing each other at one point would thus be obtained. The crossing-point would be at the left of the summit of the curve shown in Figure 2, with the iron concentration lower than 15.0 p.p.m., and at the right with the iron concentration higher than 15.0 p.p.m. That indicates a definite interrelation between the elements iron and manganese in plant nutrition.

The curve shown in Figure 3 represents the effect of various concentrations of iron in the nutrient solution on the growth of soybeans, with the manganese concentration constant at 1.0 p.p.m. If both manganese and iron were variable, a series of curves either closer to the horizontal line or farther from it would be obtained. They would be closer to the horizontal line with the manganese concentration lower than 1.0 p.p.m., and farther from it with the manganese concentration higher than 1.0 p.p.m. That also indicates a definite interrelation between iron and manganese in plant nutrition.

As seen in Table 2, the severity of manganese toxicity decreases as the iron concentration is increased in the nutrient solution. Therefore, the fact that the content of iron in the soil solution is quite variable, even in soils having approximately the same pH value, may explain why a con-

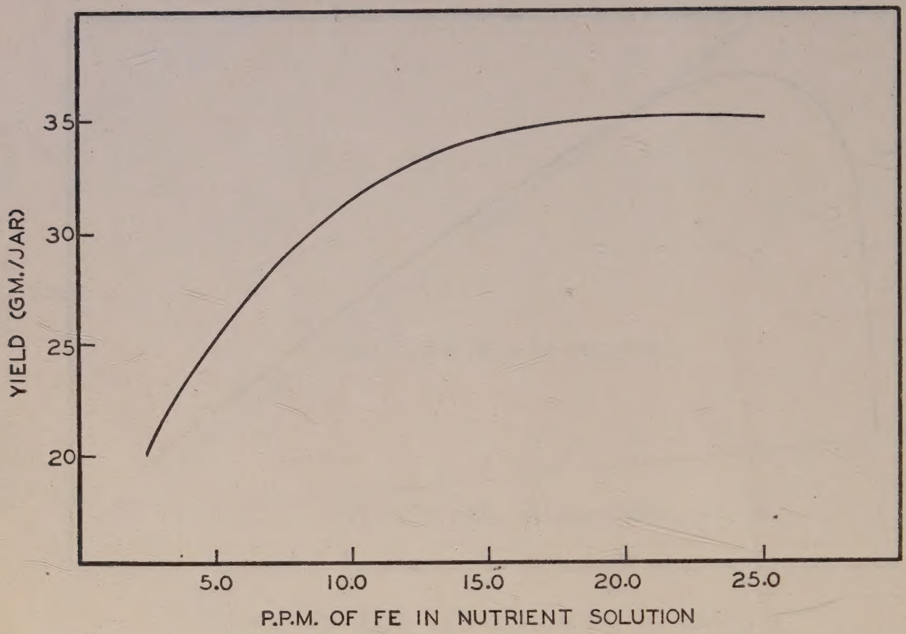

FIGURE 3. Influence of the iron concentration in the nutrient solution on the yield of soybeans (manganese constant at 1.0 p.p.m. in the nutrient solution).

centration of 2.0 p.p.m. of manganese in the solution of one soil is toxic to potatoes while the same concentration in the solution of another soil of about the same nature is apparently non-toxic.

It was found in this work that soybeans could grow without nutritional abnormalities in nutrient solutions in which the ratio of iron to manganese ranged from 5 : 1 to 100 : 1, providing that the concentration of manganese in the nutrient solution was kept above 0.1 and below 2.5 p.p.m., and the iron concentration kept above 2.5 p.p.m. However, it appears that, in order to obtain maximum yields, the ratio of iron to manganese has to be kept within narrower limits than those allowed to avoid nutritional abnormalities. It is well to note that the above statements are applicable to the entire growth period of the plants, and that the same might not be true of plants during their early growth period only.

SUMMARY

The importance of iron and manganese and the apparently conflicting data in the literature concerning the relationships between iron and manganese in plant nutrition suggested the need for the present investigation. Thus, the purpose of this investigation was to study the effect of various iron and manganese concentrations and various ratios between these two elements in the substrate on the growth of plants. The work has been done in the greenhouse, the substrate utilized was the Hoagland-Berger nutrient solution, and the soybean was chosen as the indicator plant. The results obtained may be summarized as follows:

(1) A concentration of 2.5 p.p.m. of manganese in the nutrient solution was toxic to plants when the iron concentration was low, and not

toxic when the iron concentration was high. No iron toxicity was observed with soybeans, even with 60 p.p.m. of this element in the nutrient solution. Manganese deficiency was brought about by increasing the iron concentration in the nutrient solutions having low manganese concentrations.

(2) The rate of uptake of manganese by soybeans is very nearly proportional to the supply of this element in the nutrient solution, whereas the rate of uptake of iron remains approximately constant when the concentration of this element in the tissue reaches about 300 p.p.m.

(3) Soybeans grew without nutritional abnormalities in nutrient solutions in which the ratio of soluble iron to soluble manganese ranged from 5 : 1 to 100 : 1, providing that the concentration of manganese in the nutrient solution was above 0.1 and below 2.5 p.p.m., and the iron concentration above 2.5 p.p.m. However, maximum yields were obtained with ratios lying within narrower limits than those allowed to avoid nutritional abnormalities.

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CULM, CROWN AND ROOT DEVELOPMENT IN OATS AS RELATED TO LODGING[1]

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Resistance to lodging is an important consideration in any cereal breeding program. Cereal breeders have recognized the significance of "strength of straw" but there has been a lack of knowledge concerning the association of characters which enable a plant to resist lodging. On the basis of general field observations alone, the breeder has met many difficulties in attempting to determine the plants or lines which actually possess resistance. Environmental variations from year to year and lack of a suitable lodging index have made it difficult to select the non-lodging types in the early generations.

Many studies have been conducted on the problem of lodging in cereals. A wide range of plant characters were investigated and several techniques for determining lodging resistance have been proposed. Many contradictory results were reported. This, no doubt, was due to the use of different techniques, to the influence of many different environments and to results based on the performance of too few varieties. It was the purpose of this investigation to further evaluate the factors which logically may be associated with standing ability.

Two types of lodging take place in cereal crops. One type is characterized by a breaking of the culms a few inches above the ground level. This is particularly important after the plants are ripe. The other involves leaning and bending of the culms and uprooting of the plants in the green condition. This is the more common type and frequently it occurs during a heavy rainstorm. The bending of the culms usually takes place at the surface of the soil and appears to be due to poor anchorage and weakness in the basal parts.

The plant characters, which were investigated, were considered to be those associated with lodging prior to maturity. The study was restricted mainly to a varietal analysis of the crown portions of the plants under different environmental conditions. The crown comprises the basal portions of the culms and includes secondary culms which arise from axillary buds at the basal nodes of the main axis and lateral culms. In certain places, in the text, the crown is referred to as this complex unit even though it was found to be more feasible to measure the individual parts rather than the whole crown area. Hence, particular attention was devoted to the development of the adventitious or coronal root systems, and the basal part of the culms. The term "coronal roots" refers to the roots which arise in the intercalary meristems at the bases of the crown internodes of the primary stem and its tillers. The seminal root system was not considered.

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[1] Contribution No. 158 from the Cereal Division, Experimental Farms Service, Canada Department of Agriculture, Ottawa, Canada. Some of the data reported herein formed part of a thesis submitted to the Graduate School of the University of Wisconsin in 1947 in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

[2] Senior Cerealist.

Normally, during the course of such studies, there are years when no differential lodging occurs. This prevents the evaluation of varietal measurements. In contrast to years when no lodging occurs, there are years when lodging is so severe that all gradations of resistance or susceptibility are immeasurable. Hence, the correlation of plant measurements with actual field lodging notes was not considered to be the correct method of approaching the problem. A great deal was known about the lodging behaviour of certain varieties. Outstanding examples of resistant and susceptible varieties, along with intermediate ones, were selected to evaluate plant characters which might be associated with lodging. The degree of character expression in the known resistant varieties was compared with its counterpart in the susceptible ones in an attempt to determine the characteristics which a variety must possess to enable it to resist lodging.

The terms "strong strawed" and "weak strawed" are commonly used to denote lodging resistance or susceptibility. Such designations carry the inference that the quality of the straw is responsible for the differences in lodging. In the present study, however, emphasis was placed on the roots and crowns as well as on the culms, and the two classes of varieties utilized are referred to as being resistant or susceptible to lodging.

LITERATURE REVIEW

No attempt will be made to review in detail all the literature pertaining to the problem of lodging. Investigations during the past 50 years or more have shown, quite consistently, that lodging may be associated with heavy rates of seeding (7, 16, 20, 31, 44), culms of small diameter particularly in the basal internodes (5, 6, 16, 34, 44), an abundance of nitrogen (9, 16), lack of phosphorus (2, 31), lack of potassium (2, 16, 31, 40), an insufficient amount of strengthening sclerenchyma tissue in the culms (5, 6, 17, 34), thin cell walls (6, 12, 34, 44), and a low percentage of dry matter in the straw (34, 44). Results of other investigations have shown that there is decided disagreement if an attempt is made to associate lodging with the following: erectness of leaf (6, 24), amount of tillering (34, 44), length of straw (5, 12, 31, 34, 45), weight per unit length of culm (3, 17), breaking strength of straw (3, 39), number of vascular bundles (5, 6, 12, 17, 30, 34), and percentage of lignin (17). Other characters which have shown no consistent relationship with lodging are: yield of grain (5, 12, 25, 34), yield of straw (5), depth of seeding (7, 34), length of internodes (5, 6, 17, 34), length of sclerenchyma fibres (12), and amount of silica (5, 17, 44). The results of the above mentioned investigations have been reviewed thoroughly (5, 6, 8, 17). The present review is restricted to the literature pertaining to root and crown structure as related to the problem.

The development of the crowns and coronal roots in the small grains and their importance to lodging have not been investigated extensively. Limited studies have been reported (6, 10, 23). In several cases the opinion has been expressed that stiffness of straw was not the only factor to be concerned with in lodging but also that the anchorage of the root system was important (1, 5, 6, 10, 12, 16, 17, 20, 34, 35, 36, 37, 45). The importance of strong basal internodes has also been stressed (6, 17, 20, 27, 34, 37).

In the small grains, the only detailed studies on the importance of root development to lodging have been with oats. Caffrey and Carroll (6) demonstrated various types of root growth as correlated with resistance to lodging. Well developed coronal roots extending horizontally in the soil were considered important for lodging resistance. It was generally found that the stronger varieties required a greater pulling force to uproot the plants. The same authors found that depth of crown was to some extent influenced by environmental conditions. Shading and high temperature brought the crowns close to the soil surface, while bright sunshine and cool weather had the opposite effect. The differences in depth were, however, not great. It was mentioned that, contrary to the commonly held view, depth of sowing was of little importance in determining the depth of the main coronal anchor roots of the oat plant. In the early stages of development varieties differed in the amount of cortical thickening in the coronal roots. At full development there was as great a variation between roots of the same plant as between roots of plants of different varieties. It was stated that hybridization among varieties had shown that form of root growth was controlled by genetical factors.

Derick and Hamilton (10) studied varietal differences in root development in oats. They concluded that good root development, with substantial anchorage, was an important varietal characteristic in resisting conditions which were favourable to lodging. The coronal roots of the resistant varieties were not only greater in number but were coarser and spread more extensively than those of the susceptible varieties. The former also had a smaller ratio of tops to roots.

In 1912, the Howards (23) emphasized that for lodging resistance in wheat it was necessary to have stiffness of straw combined with a strong root system. They studied the inheritance of standing ability in a cross between two wheats and stated that definite differences appeared in the F_2 generation. No actual figures or ratios were furnished.

Ramiah and Dharmalingam (34) considered lodging at the ground level in rice to be due to poor root development.

Results have been published on the relationship between type of root development and lodging in corn. Hall (4) found that the size of the brace roots was not correlated with lodging. Lodging was correlated with the pounds of force required to pull the plants from the soil and with depth, width and volume of root clump. Koehler (26) found that erect strains of corn had twice the volume of root system of those known to lodge.

Webb and Stephens (42) suggested that, under certain cultural and environmental conditions, wheat varieties differed in their ability to form roots. Late spring sowing, when temperatures were high, caused the crowns to form closer to the soil surface than did early spring or fall sowing. Deep sowing or high temperatures caused an elongation of the second and third internodes above the coleoptile node. They considered depth of crown formation in wheat to be a varietal characteristic which was greatly influenced by environment, especially soil temperature.

The importance of a well anchored plant to lodging resistance has been emphasized by Robinson (36) in Wales. In a report from the Wheat Research Institute (1) of New Zealand it was stated that: "Lodging

under our conditions is not solely a matter of strength of straw. The bending usually does not take place in the straw, but at the ground-level, and is affected by the root hold and the shape of the whole plant just where it leaves the ground." Robb (35) in Scotland reported that, in lodging, the oat culms were not always bent or broken but may be tilted over from their upright position, at the surface of the ground, through the inability of the roots to maintain the mature plants in an erect position. In selection, preference was given to plants having strong and well spread roots. Several other workers have expressed the same opinion about the apparent need for good plant anchorage.

Thus, there has been much evidence to suggest that cereal varieties vary structurally below ground as well as above and that the extent to which coronal roots provide anchorage for the plants may be one of the larger factors determining differences in lodging behaviour.

MATERIALS AND METHODS

The field experiments were conducted at the Central Experimental Farm, Ottawa, during 1947-49 and at 7 branch stations of the Experimental Farms Service as listed below. Preliminary investigations (18) at one location had shown that varietal differences in type of root growth and other plant characters could be distinguished and associated with lodging behaviour. It was realized that in order to ascertain the value of such plant characters for selection purposes, one must study their degree of expression and variation under a wide range of soil and climatic conditions. Hence, stations were chosen which varied in location from the Atlantic to the Pacific coasts and where lodging was a common occurrence.

The stations are listed below together with a description of the type of soil on which the tests were grown and a record of the total precipitation for the months of May, June and July in each of the 3 test years. The wide range of soil conditions under which the tests were grown and the variations in precipitation between both locations and years are evident. Mean maximum and mean minimum air temperatures during the growing season are not given, since they only illustrate again that the tests were conducted under a wide range of environmental conditions.

Station	Soil	Precipitation (inches)		
		1947	1948	1949
Nappan, N.S.	Nappan clay loam	9.2	9.9	7.1
Lennoxville, P.Q.	Coaticook silty loam	16.1	9.4	9.5
Kapuskasing, Ont.	Medium to heavy clay	9.4	9.3	6.2
Ottawa, Ont.	Manotick sandy loam	14.6	8.4	7.1
Morden, Man.	Heavy clay loam	6.4	10.1	6.7
Lethbridge, Alta.	Brown silty loam	5.1	12.3	6.0
Lacombe, Alta.	Black silt loam	7.2	8.9	7.1
Agassiz, B.C.	Silt loam	7.3	8.5	7.9

Eight varieties of oats which had been under observation and test for several years and whose lodging behaviour was well known were chosen. A brief description of each is given in Table 1. Numbers 1-4 may be classed

TABLE 1.—DESCRIPTION OF OAT VARIETIES TESTED

Variety	Species	Lodging resistance, 1-9	Height	Maturity	Parentage	Place of origin
1. Glasnevin Ardri	*A. sativa*	1.5	Medium	Late	Glasnevin Sonas × Victory 2	University College, Dublin
2. Beacon	*A. sativa*	1.4	Medium	Early	Alaska × Gold Rain × (Legacy × Victoria) × (R. L. 453 × Vanguard)	Cereal Division, Ottawa
3. Garry	*A. sativa*	1.8	Medium	Early	Victory × (Victoria × (Banner × Hajira))	Dominion Laboratory of Cereal Breeding, Winnipeg
4. Acton	*A. orientalis*	1.4	Medium tall	Medium	Fifty Pound Black × Alaska	Macdonald College
5. Vanguard	*A. sativa*	2.3	Medium	Medium	Hajira × Banner	Dominion Laboratory of Cereal Breeding, Winnipeg
6. Dasix	*A. sativa*	4.7	Medium tall	Early	Selection from Sixty Day	Ontario Agricultural College
7. Old Island Black	*A. sativa*	4.1	Tall	Late	Unknown	Prince Edward Island
8. Don de Dieu	*A. sativa*	3.1	Medium tall	Medium	Unknown	Quebec

as resistant to lodging, number 5 as intermediate, and numbers 6-8 as susceptible. The ideal situation would be to have lodging occur in the same years when the varietal characteristics were measured. Since this was impossible it seemed best to select contrasting types, whose past lodging performance was known, and to search for the particular plant characters possessed by those varieties proven to have resistance.

The data on lodging resistance given in Table 1 are recorded on a 1-9 scale which is used throughout the Experimental Farms Service to record lodging data. The number 1 indicates that the plants were perfectly erect and 9 that they were completely flat. The number 5 indicates an intermediate condition, i.e., 50 per cent lodged while other values indicate comparable degrees of lodging. The data are based on the combined results of 15 tests in this study, where differential lodging occurred. Similar data are available from other sources since the same varieties had been grown in yield tests at many locations for several years and lodging data taken.

Each variety was grown in plots of three 10-foot rows and replicated 3 times. Row spacing was 7 inches. A Kemp V-belt seeder was used to give uniform seeding at a depth of $\frac{1}{2}$-1 inch. The rate of seeding was one bushel per acre since previous investigations (18) had shown that varietal differences were most evident and regular when plants were allowed to develop under only moderate competition. At heavy rates of seeding varietal differences were more difficult to measure while under conditions of wide spacing all plants grew so large that differences were less evident. Seed for all tests was grown at Ottawa, well graded, prepared for seeding and treated with ceresan approximately 3 weeks prior to seeding. When there was danger of rust infection plots were dusted regularly with sulphur.

It was found that the most satisfactory time at which to dig root samples was during the period between flowering and ripening. It was less satisfactory to do the sampling when the plants were fully ripe due to their more brittle condition. A suitable time to take samples was found to be approximately 20 days after flowering, that is, 10 days prior to maturity. As described by Roemer (37), this corresponds with the time found by Kossebau and Studtmann to be best for testing the standability of plants in the field by means of a Halm-Dynamometer. The average plant height in each plot was recorded at the same time. Root samples were dug from the middle row of each plot excluding border plants. An ordinary round pointed shovel was forced into the ground to its full depth (approximately 10 inches) at a point 4-5 inches from the side of the row and a clump of plants lifted out. The clump consisted usually of 15-20 plants and care was taken to remove it from a place in a row where plant spacing was uniform and of approximately the same density for all varieties in the test. Water from an ordinary garden hose was used to wash the soil from the roots. Great care was taken to not damage the coronal roots or alter their shape. After washing, the tops were removed leaving about 4 inches of stem attached. The plants were gently separated and any abnormally large or small ones (due to irregular spacing) were discarded. The loosely adhering leaf sheaths were removed and the roots spread out to dry. The thoroughly dried samples were packed loosely to prevent injury and shipped to the Cereal Division, Ottawa. Ten representative plants were selected from the sample for detailed study.

Studies on the coronal root system of many oat varieties, in the greenhouse and field during 1940-41 and 1945-47, made it obvious that a root classification system was necessary. It was impossible to make varietal comparisons between tests by description alone. It was noted that the root type produced by certain varieties was characteristically different from that produced by others and that the resistant varieties had the greatest coronal root development.

A classification system based on a 1-10 scale, representing ten root classes or types, is shown in Figure 1. The differences between types were based upon the size and degree of spread of the coronal roots and also upon the size of the basal part of the culm. Moreover, there were notable differences in the rigidity of the roots, those in the 1-4 class being particularly rigid and resistant to bending. The size and spread of the roots and the size of the culms gradually decreased toward type 10, which represented a poorly developed crown and root system. The scale represented varying degrees of plant anchorage to the soil. It was designed to cover the range in oat root types which one may encounter.

The size of the root systems in any test depended upon the conditions under which the varieties were grown. The method of classification was not based on size of root system but on comparative differences in development. For a given set of samples it was necessary to get, first, a general picture of the material and then, by means of the scale, to measure the relative differences which existed. A particular root was assigned the value of the type it most closely resembled. The scale proved satisfactory as a means of comparing the coronal root systems of the different oat varieties in the various tests.

In addition to classifying the samples on the basis of root type, the number of coronal roots was counted and the diameter of the main culm measured by means of a micrometer caliper at a point approximately one inch above the soil level. In analysing the data on root type, no transformations were necessary since plant variations were practically the same, regardless of what part of the scale was being used.

EXPERIMENTAL RESULTS

Varietal Differences in Root Type

Following germination, elongation of the first internode brings the coleoptile node to a position just below the soil surface. After the young shoot appears above ground the first pair of adventitious roots appear in the region of the coleoptile node (19). Later the adventitious roots develop above the cleoptile node in the intercalary meristems at the bases of the internodes. Figure 2 is an enlarged view of the crown region showing the whorls of adventitious roots arising from the crown nodes. It is by means of these roots that each plant is anchored to the soil. Roots arising from the above-ground nodes may be commonly noted. They may or may not enter the soil and do not appear to contribute to plant anchorage.

Observations and measurements on more than 10,000 oat plants grown at several locations during the past 5 years have shown that varieties differ in the general type of adventitious root system which they produce. Varieties which possessed a high degree of lodging resistance generally

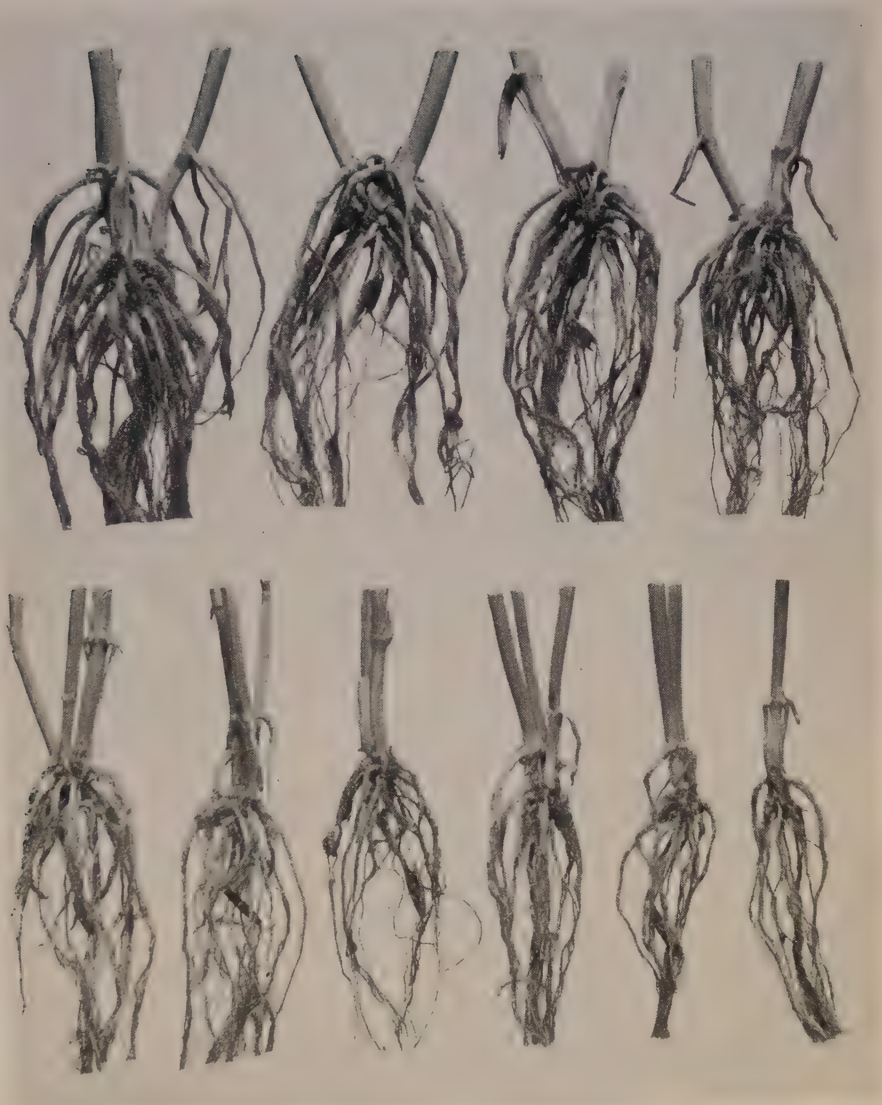

FIGURE 1. Scale by which oat roots were classified on a basis of 1-10. *Upper row*, types 1-4. *Lower row*, types 5-10. Roots are comparable in size to types produced at ordinary rates and depths of seeding.

FIGURE 2. Enlarged view of basal culm region showing whorls of adventitious (coronal) roots arising from crown nodes.

produced large, widely spreading and rigid coronal roots. Varieties which were susceptible to lodging had smaller and more flexible roots which had a greater tendency to grow downward in the soil, thereby affording an inferior type of anchorage. This is well illustrated in Figure 3. Although differences of this magnitude were not revealed consistently each year at each location, wide differences were noted frequently.

In Figure 4 the average root type of the 8 varieties is shown for each location and year. The conclusions which may be drawn from an analysis of these data are: (1) That in any one year the root type of a particular variety varied considerably from one location to another, for example, in 1947 the average root type for G. Ardri varied from 2.8 at Lethbridge (irrig.) to 4.9 at Kapuskasing. (2) That the varietal variation from place to place did not follow a regular pattern each year. (3) That root type is a varietal characteristic which, although showing considerable variation, tended to be restricted within certain limits. For example, Acton consistently produced a very superior type of root development which varied from type 2-4. In contrast, Don de Dieu consistently produced a poor type of root development which varied within the limits of 4.5-7.5. (4) That the 4 varieties on the left which are resistant to lodging had a much better development of coronal roots than the 2 susceptible varieties on the right. The intermediate variety Vanguard occupied an intermediate position with regard to root type. The variety Old Island Black, while susceptible to lodging, produced a fairly good type of root anchorage. However, it will be noted later that this variety is inferior in the development of other characters which are important to lodging resistance.

The tendency for Beacon to produce a much poorer root system at Lennoxville in 1947 was due partly to the presence of a moderate infection of Victoria blight caused by *Helminthosporium victoriae* Meehan and Murphy.

In Figure 5, the results for the 3 years have been averaged. It illustrates again the marked tendency for each variety to have a particular root type at all locations. It shows clearly that, although root type varies from place to place, comparable varietal differences were maintained at each location and in such a manner that the lodging resistant varieties may be separated from the lodging susceptible ones.

Many observations have been made to determine if differences in root type could be measured adequately at earlier stages of growth, for example, at the fifth or sixth leaf stage. Varietal differences were evident at the younger stages but not nearly so pronounced as later; also there was a greater variability between plants of the same variety.

Although varietal differences in root type seem very evident it would be difficult to always distinguish, with certainty, the resistant from the susceptible varieties on this basis alone. Many varieties would be classified correctly but there would be confusion with varieties like Beacon and Old Island Black, both of which have somewhat similar root types but differ greatly in actual resistance.

The correlation coefficient between root type and number of coronal roots using variety station means from all tests was $r = -0.469$ (1 per cent level of significance $= 0.138$). The correlation was highly significant, indicating that varieties with a better root development tended to have a

greater number of coronal roots and vice versa. Between root type and culm diameter the value of r was -0.415. This indicated that varieties with the largest culms tended to have better development of anchor roots. Exceptions were noted but oat varieties which produced large culms also tended to produce large, widely spreading and rigid coronal roots and a greater number of roots. It showed that a plant with a sturdy form of development above ground also usually had a sturdy type of development below ground.

Varietal Differences in Culm Diameter

The average culm diameter, in millimeters, for the years 1947-49 for all varieties at each location is given in Figure 6. It represents the diameter of the basal part of the main culm at a position $\frac{1}{2}$-1 inch above the soil level. In nearly every test varietal differences were highly significant. The culm diameter varied greatly from one location to another. This was true for all varieties. Proceeding from the lodging resistant varieties on the left to the susceptible varieties on the right, one notes that the culm size or diameter gradually decreases.

Apparently it would not be too difficult to separate lodging resistant varieties from susceptible ones by classifying them according to culm diameter. However, on the basis of size alone it might be difficult to distinguish grades of resistance or susceptibility. Similar to root type, it does appear to be a varietal characteristic associated with lodging resistance and one whose degree of expression is conditioned by environment. The important point is that, at all locations, varietal differences on a comparable basis may be detected readily.

A highly significant positive correlation coefficient of $r = +0.849$ was obtained between diameter of culm and number of coronal roots when the means for each variety and year at the 9 locations were used; thus, varieties with the greatest diameter of culm also had more coronal roots. When variety means for all years and tests were compared, there were exceptions, such as Beacon and Garry, which had similar culm diameters but a different number of roots. Also Don de Dieu had as large or larger culms than Old Island Black but fewer roots. The correlation further established the importance of culm diameter as an indicator of root anchorage. A similar relationship was reported in corn (28) wherein the number and size of the permanent roots were correlated directly with the size of stalk.

Varietal Differences in Plant Height

Plant height varied extensively between locations as did the other characters measured. This is illustrated in Figure 7. There was no readily noticeable trend for the resistant varieties to be short and the susceptible varieties to be tall. However, the resistant variety Beacon does tend to be fairly short and the susceptible variety Old Island Black is usually tall. Both Ardri and Acton, two resistant varieties, were tall and even as tall or taller than the very susceptible variety Don de Dieu. Undoubtedly, from a mechanical standpoint, height does affect the standing ability of oats. As stated by Roemer (37) short straw will aid in assisting varieties to remain upright, but it is by no means linked with lodging resistance; nor

FIGURE 3. *Left to right:* Typical root type of the lodging resistant oat variety Acton and the susceptible variety Dasix grown at Agassiz, B.C., 1948.

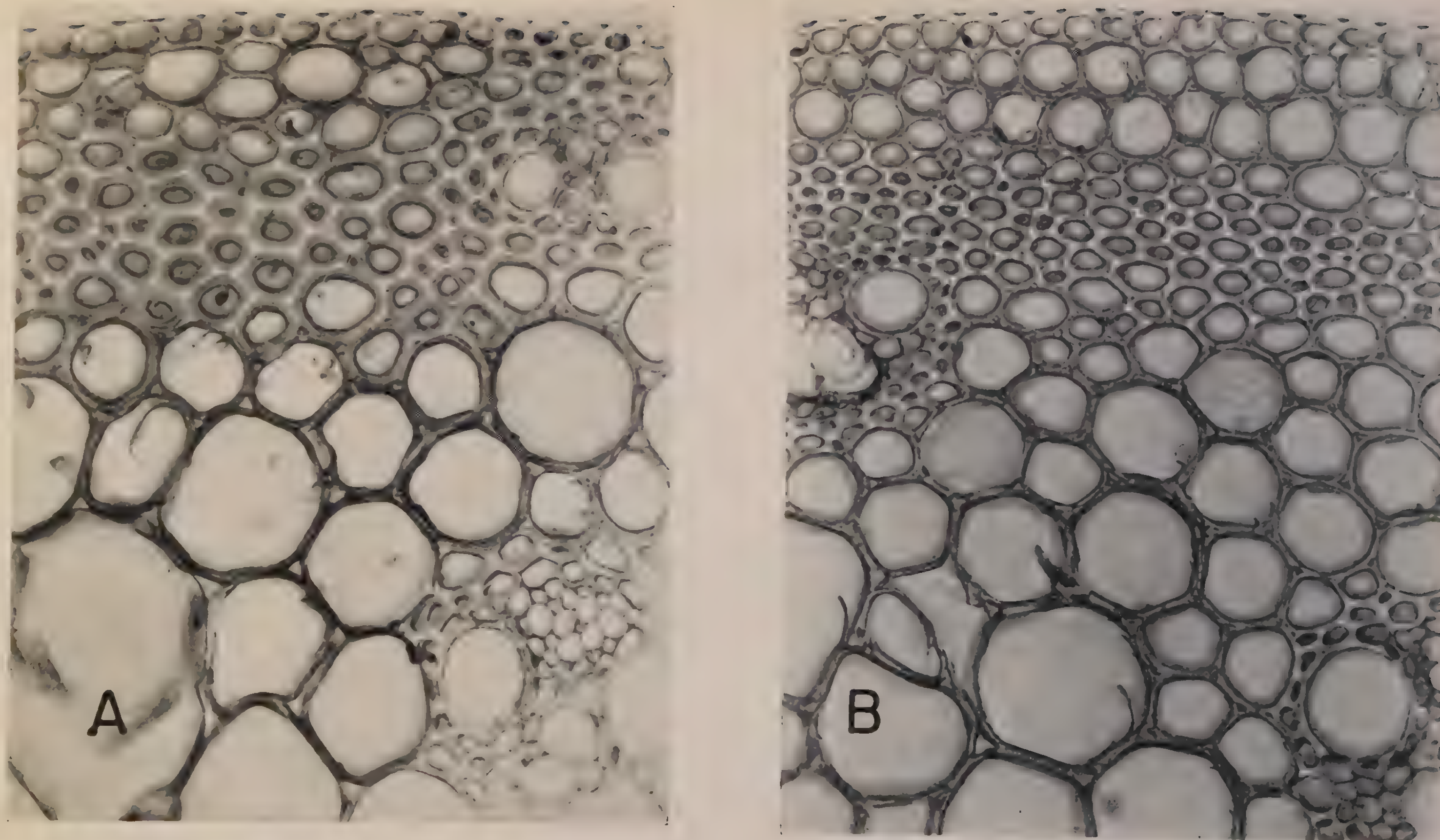

FIGURE 9. Cross section of the culm, one-half inch above soil level in two oat varieties. A, the lodging resistant variety Clinton. B, the susceptible variety State's Pride. X165.

is tall straw always associated with lodging susceptibility. It seems therefore, that one should not attempt to associate height alone with the problem of lodging.

Varietal Differences in Number of Coronal Roots

As shown in Figure 8, and as found in previous experiments (18), there was a highly significant varietal difference in number of coronal roots. The number of roots varied with location. This was particularly evident at Agassiz where a low number of roots was produced. Differences between varieties tended to follow the same trend at all stations. In general, the resistant varieties had more coronal roots than the susceptible varieties. However, the difference was not great between Beacon, Vanguard and Old Island Black. If only a few varieties had been studied, for example, Garry, Acton, Don de Dieu and Dasix, one might have concluded that the character could serve as part of a lodging index. If a still greater number had been studied, possibly more examples would have been found where differences between resistant and susceptible varieties were slight. This character by itself does not appear to be of great value in distinguishing lodging resistant types.

In one experiment (18) wherein the plants were sown 12 inches apart each way, the results indicated a relationship between the number of coronal roots and lodging resistance, that is, the greater the number of coronal roots the greater the resistance to lodging.

Varietal Differences in Number of Tillers

There were differences between varieties in the number of tillers produced and also the number varied with the location at which the plants were grown. Again, the general varietal pattern was much the same at all stations, illustrating that the differences between stations were the effect of environment on the expression of a varietal characteristic.

It did not follow that varieties which tillered the most always had the greatest number of coronal roots. Acton had many coronal roots but not a high number of tillers. Vanguard tillered more than Acton but had fewer coronal roots. Don de Dieu produced as many tillers as Vanguard but fewer roots.

If one were to make comparisons between the lodging resistant varieties alone it would seem that varieties which tillered less had larger culms, but if comparisons were made between Garry and Old Island Black or Ardri and Dasix, for example, then no such indication existed. Garry had both larger culms and more tillers than Old Island Black. Ardi and Dasix tillered much the same at several stations but the former had much larger culms.

Differences in tillering do not separate the varieties into resistant and susceptible types and hence the character is not considered to be of value as part of a lodging index.

Lodging Index

Many attempts have been made to find an index to lodging in order that plant breeders may have some character or association of characters to look for and feel assured that the plants or lines with the greatest

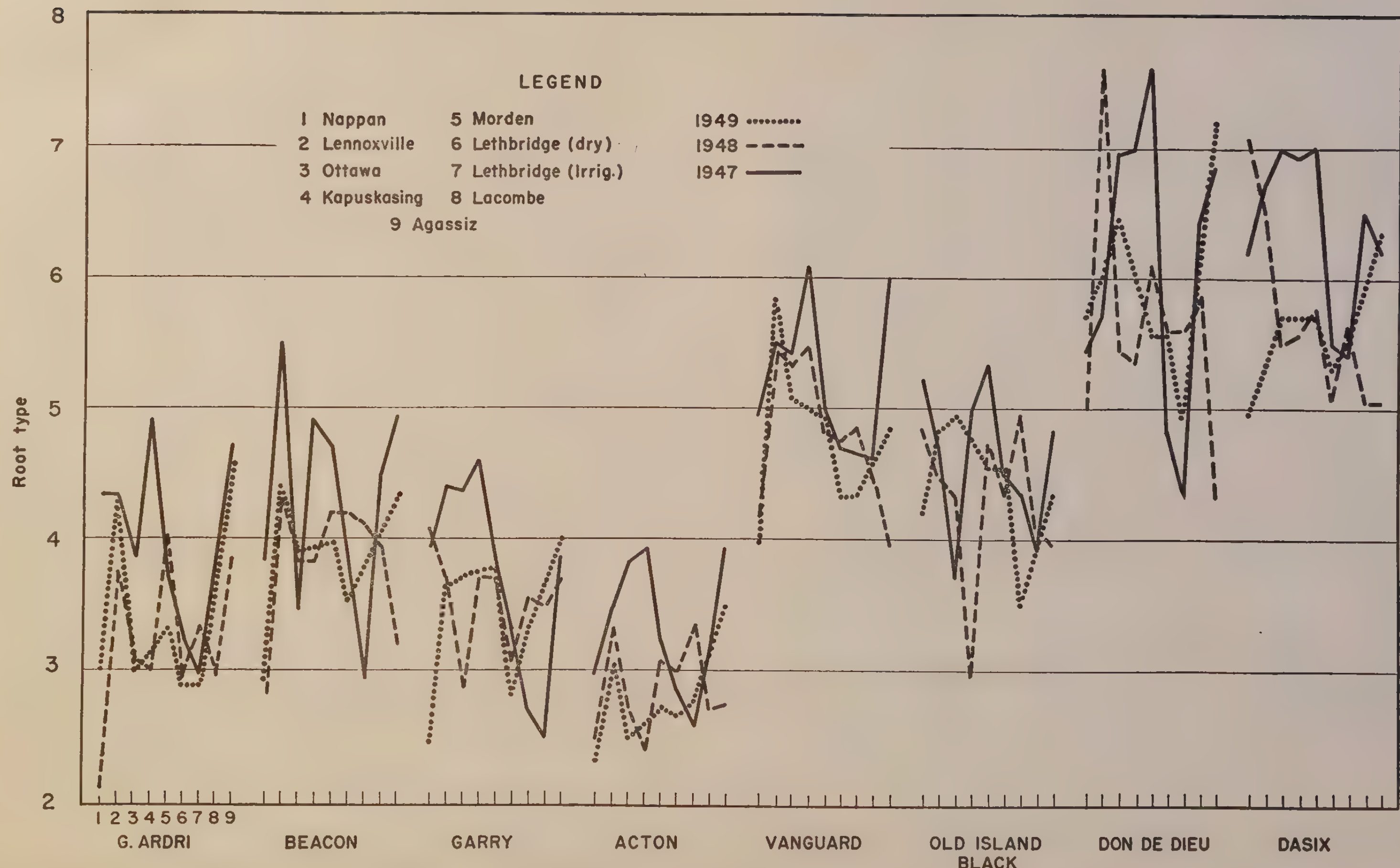

FIGURE 4. Average root type (1-10 scale) of eight oat varieties, in each test, at eight stations for 1947, 1948 and 1949.

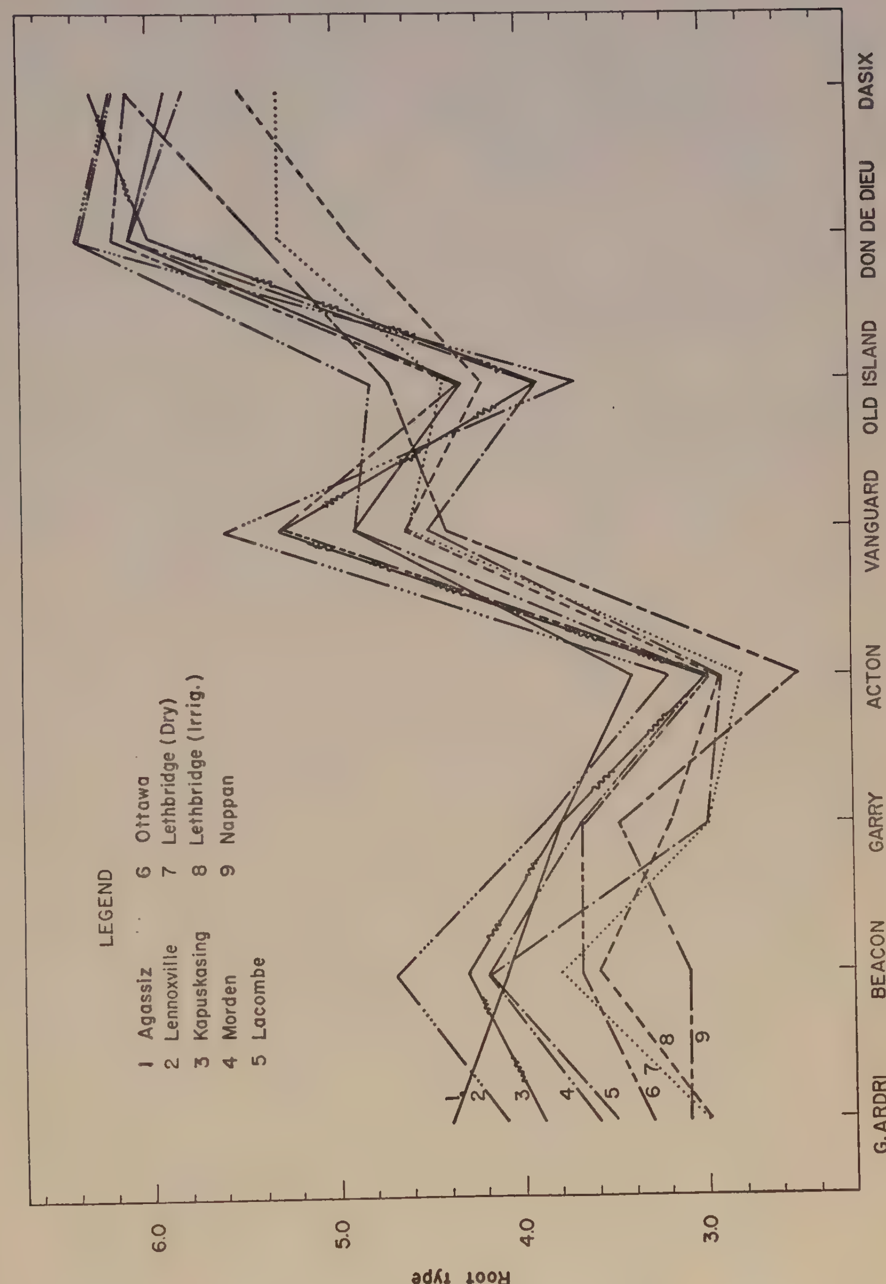

FIGURE 5. Average root type (1-10 scale) of eight oat varieties grown at eight stations during 1947-49.

TABLE 2.—THE DISCRIMINATE FUNCTION EQUATIONS OBTAINED FROM ANALYSING DATA ON 7 OAT VARIETIES AT 8 LOCATIONS FOR 3 YEARS[1]

Location	1947	1948	1949
Nappan	$-5.3 X_1 + 11.7 X_2 - 1.0 X_3$	$-4.1 X_1 + 4.1 X_2 - 1.0 X_3$	$-5.5 X_1 + 1.0 X_2 - 1.1 X_3$
Lennoxville	$-10.1 X_1 + 1.0 X_2 - 2.2 X_3$	$-1.9 X_1 + 8.5 X_2 - 1.0 X_3$	$-6.1 X_1 + 1.0 X_2 - 1.0 X_3$
Ottawa	$-2.3 X_1 + 4.4 X_2 - 1.0 X_3$	$-6.1 X_1 + 8.3 X_2 - 1.0 X_3$	$-4.7 X_1 + 5.5 X_2 - 1.0 X_3$
Kapuskasing[3]	$-5.1 X_1 + 4.8 X_2 - 1.0 X_3$[2]	$-2.4 X_1 + 20.8 X_2 - 1.0 X_3$	
Morden	$-1.2 X_1 + 2.9 X_2 - 1.0 X_3$	$-4.6 X_1 + 8.3 X_2 - 1.0 X_3$	$-3.6 X_1 + 6.5 X_2 - 1.0 X_3$
Lacombe[3]	$-1.8 X_1 + 13.1 X_2 - 1.0 X_3$	$-4.3 X_1 + 9.2 X_2 - 1.0 X_2$	
Lethbridge—dry	$-9.9 X_1 + 10.1 X_2 - 1.0 X_3$	$-4.1 X_1 + 0.9 X_2 - 1.0 X_3$	$+5.0 X_1 + 1.0 X_2 - 1.1 X_3$
Lethbridge—irrig.	$-3.8 X_1 + 18.3 X_2 - 1.0 X_3$	$-10.8 X_1 + 4.9 X_2 - 1.0 X_3$	$-3.1 X_1 + 42.5 X_2 - 1.0 X_2$
Agassiz	$-5.3 X_1 + 14.0 X_2 - 1.0 X_3$	$-9.0 X_1 + 11.0 X_2 - 1.0 X_3$	$-8.9 X_1 + 1.0 X_2 - 2.1 X_3$
Mean of 8 tests	$-5.0 X_1 + 9.6 X_2 - 1.1 X_3$	$-5.4 X_1 + 8.3 X_2 - 1.0 X_3$	
Mean of 6 tests			$-5.6 X_1 + 2.8 X_2 - 1.2 X_3$

[1] X_1 = root type, X_2 = diameter of culm and X_3 = height of plant.
[2] Discriminate function not significant.
[3] Test damaged by adverse weather in 1949.

lodging resistance were being chosen. Only rarely can one select wisely, in early generations, on the basis of actual field performance. Although many plant characters have been proposed as suitable lodging indices, plant breeders have not found any one index to be sufficiently practical or reliable to merit extensive use. In a previous paper (17) it was suggested that a suitable index, based on observable plant characters, might be arrived at by expressing in one figure the combined effect of two or more characters. In other words, a suitable lodging index must be based on the effect of more than one character. A possible index was given by dividing the average height of the main tillers by one-tenth the diameter of the culm. This was based on the finding that both a tall plant and a thin culm induced lodging and could be represented jointly by a high index number.

From studies made since 1945, it was realized that an index must include the effect of coronal root type in addition to the effect of plant height and culm diameter. Moreover, a suitable index must give a correct weighting to each character incorporated, i.e., the relative contribution of each character must be included in the index figure.

In order to devise a lodging index for each variety by combining the values for the 3 characters, root type, diameter of culm and height, and in order to be able to allot a correct proportionate value for the contribution of each character, the discriminate function analysis was used (14). Only the data for the 4 resistant and 3 susceptible varieties were analysed.

In Table 2 the discriminate function equations are listed for each location in each year. With few exceptions, there was considerable similarity in the values of X_1, X_2, and X_3 at the different locations and in different years. The order of importance of the three characters in contributing to lodging resistance was diameter of culm, root type and height. As an approximate general average for all tests their relative importance may be given numerically as 10 : 5 : 1, respectively. This assumes, of course, that diameter of culm is measured in millimeters, root type on a scale of 1-10, and height in inches.

Table 3 shows the lodging index figure which was calculated for each variety at 3 widely separated locations during 1947-1949. The lodging resistant group of varieties may be readily differentiated from the susceptible group by this index. Similar results were obtained for the other 6 locations. The index figure is calculated as in the following example. At Nappan in 1947, Ardri had a culm diameter of 4.3 mm., a root type of 4.3, and was 45.0 inches tall. By substituting in the discriminate function equation one calculates the index to be $(+ 11.7 \times 4.3) + (- 5.3 \times 4.3) + (- 1.0 \times 45.0) = 17.5$. The index figures, which were calculated by using the discriminate function equations were compared with those obtained by dividing the height by one-tenth the culm diameter. The former were found to give a better differentiation between varieties.

It would be desirable to include actual and reliable field lodging data for the same locations and years for which the index is given. However, weather conditions were such that reliable lodging data were not obtained at any one location for each of the 3 test years. This again re-emphasized the difficulty of attempting to compare plant measurements with actual lodging data.

TABLE 3.—LODGING INDEX[1] FOR 3 LODGING RESISTANT AND 3 SUSCEPTIBLE OAT VARIETIES GROWN AT 3 LOCATIONS FROM 1947-1949

Variety	Nappan			Ottawa			Agassiz		
	1947	1948	1949	1947	1948	1949	1947	1948	1949
Lodging Resistant Varieties—									
G. Ardri	17.5	38.5	66.9	13.1	35.9	35.7	23.8	41.2	130.2
Acton	17.4	46.4	63.9	14.2	36.3	36.3	22.5	44.3	127.9
Garry	14.6	41.8	63.7	16.9	34.5	34.4	27.5	38.7	122.9
Lodging Susceptible Varieties—									
Old Island Black	39.2	59.6	80.0	24.0	57.5	52.9	43.1	58.9	152.1
Don de Dieu	33.5	54.3	82.5	28.8	56.9	52.4	48.0	54.8	155.9
Dasix	36.6	58.5	79.2	23.7	55.5	49.7	38.7	57.5	149.1

1. Lodging index based on discriminate function whereby relative value of root type, diameter of culm and height is assessed. Figures have minus value.

TABLE 4.—AVERAGE DATA ON 8 OAT VARIETIES GROWN AT 8 LOCATIONS DURING 1947-49

Variety	Height, inches	Diameter of culm, mm.	Root type, 1-10	Lodging index[1]	Number of coronal roots	Number of tillers	Lodging resistance, 1-9
G. Ardri	45.9	3.8	3.5	48.6	24.2	2.1	1.5
Beacon	41.0	3.5	4.0	47.5	23.4	2.6	1.4
Garry	43.3	3.4	3.5	49.5	26.8	3.0	1.8
Acton	47.1	3.5	3.0	47.5	29.8	2.4	1.4
Vanguard	42.9	3.2	4.9	57.6	22.6	2.7	2.3
Old Island Black	51.0	3.2	4.2	59.9	23.4	2.4	4.7
Don de Dieu	46.0	3.2	5.9	61.4	20.4	2.5	4.1
Dasix	43.9	3.1	5.9	59.8	21.5	2.5	3.1

[1] Based on discriminate function equation calculated for each location and year.

Table 4 shows the summarized data for all varieties, at all stations, for the 3 years. The following points may be noted: (1) That all resistant varieties are not short strawed nor are all susceptible varieties tall. (2) That the resistant varieties have larger culms. (3) That resistant varieties have a better development of coronal roots. (5) That resistant varieties usually have a few more coronal roots than susceptible varieties. (5) That number of tillers is not associated with lodging resistance. (6) That the lodging index separates the varieties into susceptible and resistant classes.

Rate and Depth of Seeding

In 1946, field tests were conducted at the University Farm, Madison, Wisconsin, to determine the effect of a heavy and light rate of seeding and a shallow and deep depth of seeding on the plant characters which are associated with lodging resistance. The rates of seeding were 1 and 3 bushels per acre while the depths were $\frac{3}{4}$ inch and 3 inches. The 4 varieties, Glasnevin Ardri, Beacon, Old Island Black and Dasix, were tested.

During the first 2 weeks after emergence, the plants in the deeply sown plots were more spindly and lighter green in colour than those which had been seeded shallow. At the end of 6 weeks of growth the plants in deep seeded plots had not become so well established as those in the shallow seeded ones. In order for the plants to emerge from the soil there was great elongation of the first internode. The coleoptile node was elevated to a point $\frac{3}{4}$-$1\frac{1}{2}$ inches below the soil level. Elongation of the second internode enabled the crown to form only slightly lower in the soil than would have been the case had the seedling depth been normal. A similar observation was made by Caffrey and Carroll (6).

Differences in root type between the 2 rates were highly significant, the better root type being produced at the thinner seeding. Shallow seeding produced better root development than deep seeding, the differences being highly significant. This was not always so in a date of seeding experiment when the root type was often as good or better at the 3-inch depth when seeded late. This may have been due to a drier soil condition which possibly favoured the deeper seeding.

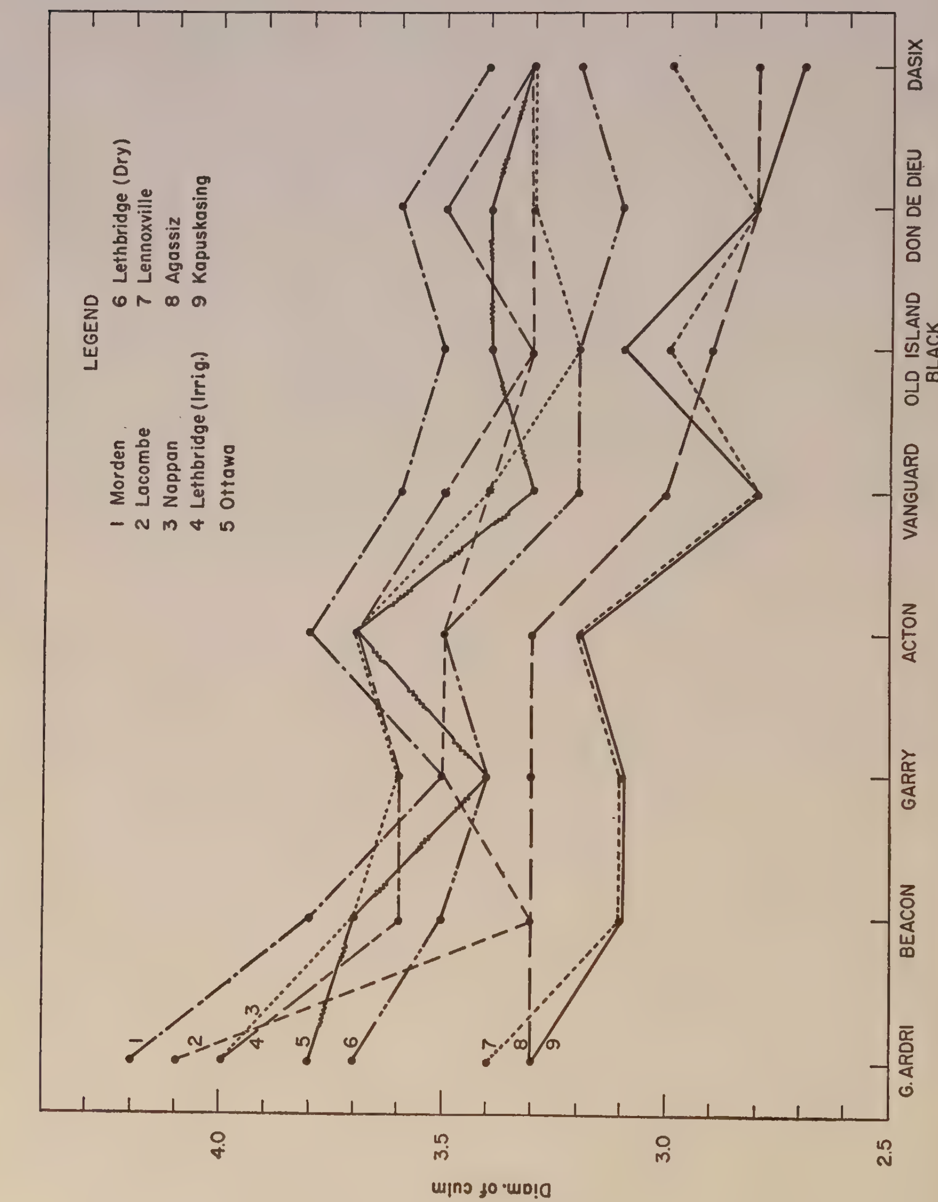

FIGURE 6. Average culm diameter, in millimetres, of eight oat varieties grown at eight stations during 1947-49.

Significantly larger culms were produced at the 1 bushel per acre rate than at 3 bushels. The difference was more pronounced at shallow seeding than at deep seeding. Height was not affected by depth of seeding but plants of all varieties at the heavier rate were slightly shorter than those at the lighter rate.

Except for expected variation, the varietal differences were much the same at both rates and depths of planting. In another experiment the root type, characteristic of a particular variety, was practically the same in early and late plantings although the susceptible varieties tended to produce a poorer root type under late seeding. In general, significantly larger culms were produced when seeding was early. The greatest differences between varieties were evident at the shallower depth and at 1 bushel per acre. Again, the results illustrate the consistency with which a particular root type was associated with a particular variety. The tendency for some varieties to produce an inferior root type when seeded late and also weaker culms may help to explain the observation (20) that late seeded crops often lodge more than early seeded crops.

HISTOLOGICAL OBSERVATIONS

In a previous study (17) it was found that the extent to which the internal anatomical features of the culm were developed in an oat variety may differ from one internode to another. Only the 3 lower internodes were examined. For measuring varietal differences, observations at the second above-ground internode were considered most suitable. The only anatomical feature which seemed to be consistently associated with lodging resistance was the vascular bundles, whose size and number were greatest in the resistant varieties.

In this experiment, the 5 varieties, G. Ardri, Beacon, Old Island Black, Dasix and Don de Dieu, were compared histologically in the basal part of the culm at a point $\frac{1}{2}$ inch above the soil level and in the large upper coronal roots. Material for sectioning was gathered at heading time from tests seeded at 1 bushel per acre and at normal depth at Madison, Wisconsin. F.A.A. fixative was used. Ordinary histological techniques using the butyl alcohol method were followed. Sections were cut at 80 microns and stained with safranin and fast green. Sections cut too close to the crown were unsuitable because the vascular and lignified tissue was irregular in outline. Measurements were made by means of an ocular micrometer. Data were taken on 2 cross sections on each of 4 main culms and on 2 roots from each of 5 plants.

Anatomy of the Basal Culm

The data on the anatomy of the basal culm are given in Table 5. Where significant differences between varieties were found to exist, least significant differences were recorded except for the data in columns 4 and 6. These 2 measurements were not designed to determine actual varietal differences but merely to show that differences existed.

The cross sections of the resistant variety Ardri were significantly greater in diameter than those of the other varieties. The resistant variety Beacon had a significantly greater culm diameter than 2 of the susceptible varieties but not greater than Don de Dieu.

TABLE 5.—ANATOMICAL MEASUREMENTS ON CROSS SECTIONS OF THE CULM BASE ONE-HALF INCH ABOVE SOIL LEVEL, ON 5 OAT VARIETIES

Variety	Diameter of cross section	Width of sclerenchyma layer	Distance from section periphery to sclerenchyma layer	Length and width of vascular bundles	Number of vascular bundles	Position of vascular bundles[1]
	mm.	mm.	mm.			
G. Ardri	4.42	0.26	0.12	0.28 × 0.19	48	18
Beacon	3.47	0.20	0.12	0.30 × 0.21	35	9
Old Island Black	3.19	0.12	0.11	0.22 × 0.16	32	25
Dasix	2.81	0.12	0.09	0.22 × 0.17	25	24
Don de Dieu	3.26	0.15	0.14	0.24 × 0.18	40	17
L. S. D.	0.27	0.03	0.02	—	3	—

[1] Average distance in millimeters between the tips of the bundles and the sclerenchyma layer, expressed as a percentage of the distance from the sclerenchyma layer to the inside edge of the culm wall.

The sclerenchyma layer was composed of thick walled, lignified cells near the periphery of the culm. The width of this layer in the resistant varieties was significantly greater than in the susceptible ones. In the former, the cell walls of the sclerenchyma and surrounding tissues were lignified more heavily than in the latter. Several workers (6, 12, 34) reported that strong strawed cereal varieties had thicker sclerenchyma cell walls. The proximity of the sclerenchyma tissue to the culm periphery was measured also. While small varietal differences did exist, they were not necessarily associated with resistance to lodging. This measurement was taken in light of the fact that in a column, when more of the strengthening material is placed towards the outside, the greater is its ability to withstand stresses and strains.

The vascular bundles were usually larger in the resistant varieties. This is in accordance with a previous report (17). As found by other workers, the number of bundles was greater in some resistant varieties than in some susceptible ones. However, the susceptible variety Don de Dieu had a significantly greater number of bundles than Beacon. Rather than the number of bundles alone being a varietal characteristic, it appeared from these data and as found previously (17, 28) that the number tended to be associated with the size of the culm, that is, the greater the diameter of the culm, the greater the number of vascular bundles.

Similar results were obtained when the lodging resistant variety Clinton was compared with the susceptible variety State's Pride. These structural differences are illustrated in Figure 9 (*facing page 295*). Clinton had a larger culm and a much wider sclerenchyma layer which was located closer to the culm periphery than in State's Pride. The sclerenchyma fibres were much heavier lignified in Clinton. Both varieties had essentially the same number and size of vascular bundles but those of Clinton were placed much closer to the strengthening sclerenchyma than were those of State's Pride.

The positioning of the vascular bundles may be of great interest. The figures in column 6 of Table 5 represent, in proportion to culm size, the distance which separated the sclerenchyma layer from the main ring

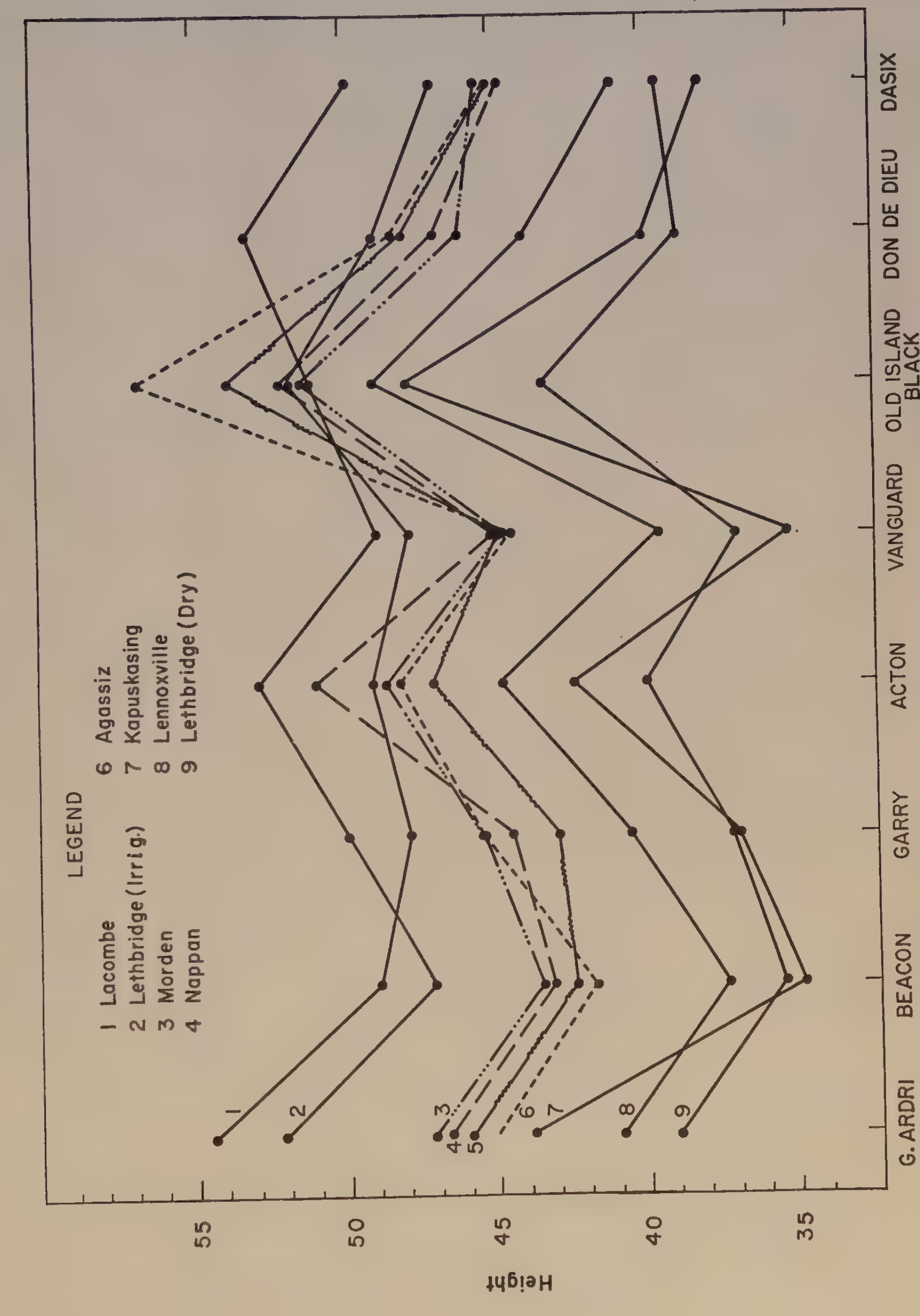

FIGURE 7. Average plant height, in inches, of eight oat varieties grown at eight stations during 1947-49.

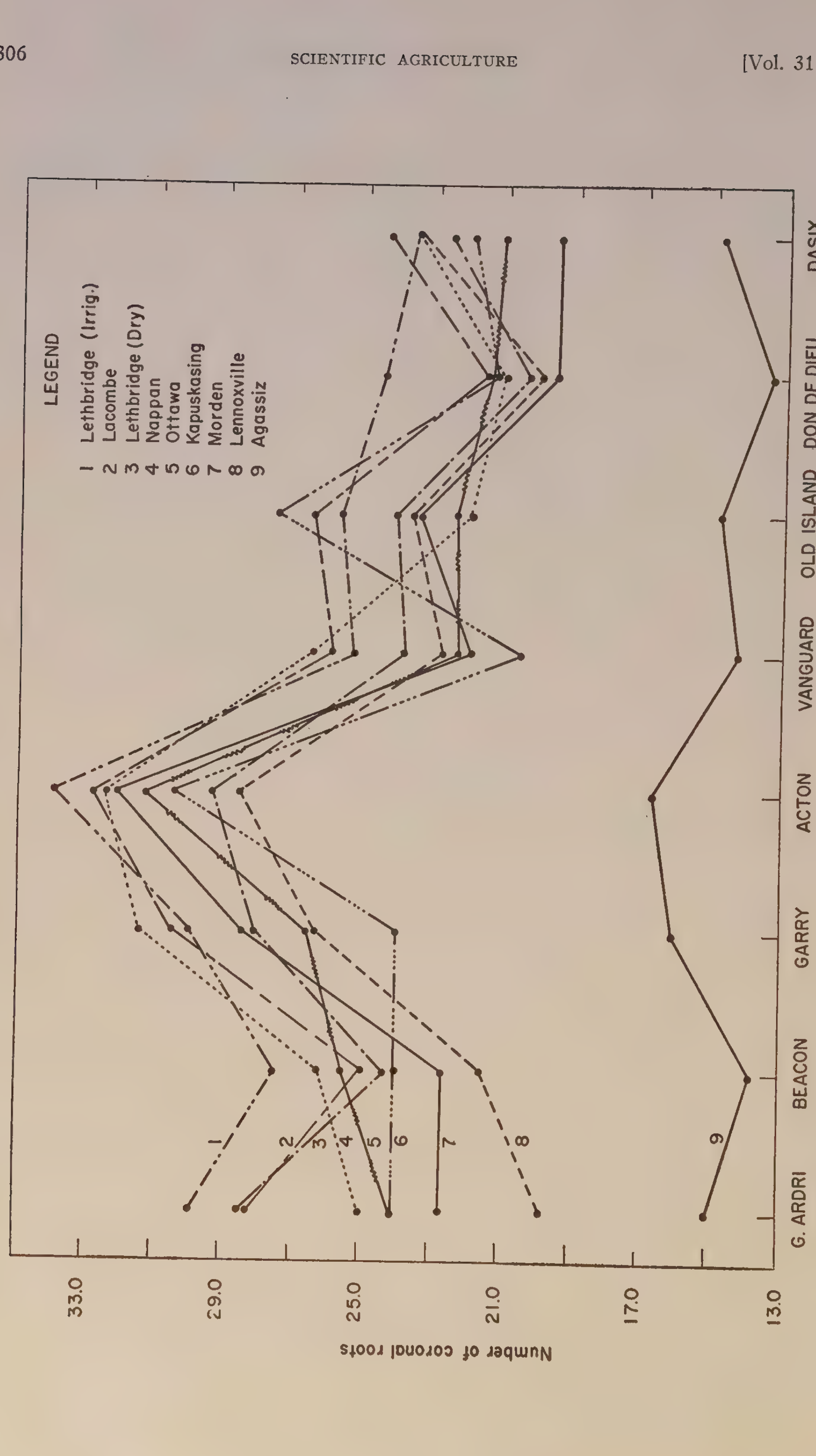

FIGURE 8. Average number of coronal roots of eight oat varieties grown at eight stations during 1947-49.

of vascular bundles. If both the sclerenchyma layer and the vascular bundles may be considered as giving support to the culm, then, if they lie very close together, their combined strengthening effect should be greater than it would be if they were separated more widely. In Beacon, the sclerenchyma tissue and the bundles were in close proximity. In the susceptible varieties they were more widely separated. The high value for Ardri did not give a true picture. The fact that it had such a large number of bundles meant that many were scattered throughout the section and since the distance to all bundles was measured, the resultant value was high. Ardri had as many vascular bundles in close proximity to the sclerenchyma layer as Beacon.

It may be mentioned that the internal structure of oat varieties was compared with resistant and susceptible wheat and barley varieties. In wheat the sclerenchyma cells were smaller, more uniform and more heavily lignified. There appeared to be slightly more sclerenchyma tissue for a given size than in oats. The strengthening tissue was located closer to the outside of the culm than in oats or barley. The vascular bundles in wheat were very uniform in size and located in a ring very close to the sclerenchyma, thereby concentrating more supporting tissue in one area and providing added strength. Both were not only in closer proximity to each other but were located nearer to the outside of the culm than in the other two cereals. The parenchyma cells were also thicker walled than in oats or barley. The concentration of strengthening tissue near the outside of the culm should give wheat an advantage in strength. This may be a significant factor in enabling wheat to have more lodging resistance than barley or oats.

Although sampling variability was quite great when individual culms were selected for sectioning, it appeared evident that resistant oat varieties had more strengthening tissue in the basal culm area and that there may be differences in positioning of the strengthening tissues thereby adding to the strength of the straw. These factors must undoubtedly contribute to the bending resistance which certain varieties possess in the lower culm regions.

Anatomy of the Coronal Roots

Portions of coronal roots, adjacent to crown nodes, were sectioned and examined histologically. The following varieties were used: Ardri, Beacon, Don de Dieu, Old Island Black, Dasix and Vanguard.

The coronal roots of each variety showed considerable variation in size and in the amount of lignified tissue. The greatest variation was between roots from different crown nodes. There appeared to be variation between roots of different ages. Generally, the lodging resistant varieties had significantly larger roots than the others but those of the intermediate variety and the susceptible ones were essentially the same size. The amount of lignified tissue in the Ardri roots was almost twice as great as in the other varieties which, in turn, did not differ from one another.

Caffrey and Carroll (6) found that in fully developed oat plants no varietal differences in structure of coronal roots could be demonstrated. In the present study variability between roots was found to be too great

Table 6.—Erectness of leaf of 6 oat varieties grown in the greenhouse and in the field

Variety	Angle between third leaf and stem (greenhouse)	Erectness of leaf (field) 0-10
G. Ardri	25° (20- 30)	9
Beacon	25° (20- 30)	8
Acton	90° (70-100)	5
Dasix	70° (40-100)	7
Old Island Black	95° (70-110)	3
Don de Dieu	90° (60-110)	4

and hence the measuring of varietal differences in root rigidity by comparing the amount of lignified tissue present in the roots does not offer much encouragement. However, it is quite possible that the greater rigidity of the general root mass of some varieties is largely due to a greater amount of lignified tissue.

Erectness of Leaf

Certain lodging resistant oat varieties, particularly Ardri and Beacon, had been observed as having very erect leaves while the opposite was true in susceptible varieties such as Old Island Black and Don de Dieu. Greenhouse and field observations were made at Madison, Wisconsin, to determine if erectness of leaf was associated with the lodging resistance of a variety. Hunter (24) found no close association between erectness of early growth and the standing ability of winter oats. Some workers have stressed the importance of leaf erectness to eliminate heavy shading and allow better development of the basal culm internodes (6, 37).

Data were recorded on greenhouse plants being grown at 16° C. and 20° C. in an experiment replicated 4 times and on which root and crown measurements were being made. The field plants were taken from the date and rate of seeding experiments described earlier. Measurements were made when the plants were in the third leaf stage and involved determining the angle between the third leaf and the stem. A protractor was conveniently used for this purpose. In the 0-10 scale used for field readings, 10 means that the leaves were very erect.

Table 6 shows the average angle of leaf erectness for 6 oat varieties grown in the greenhouse and field. In each variety the leaf angle was measured on 80 plants. The range of variation between plants is shown in brackets. Field and greenhouse results were very similar. The leaves of the resistant varieties Ardri and Beacon were much more erect than those of the other varieties. The leaves of the resistant variety Acton were very lax compared to those of the other resistant varieties. Acton grew more rapidly than the others and although the new leaves were erect, the older ones quickly became decumbent. The 2 susceptible varieties Old Island Black and Don de Dieu did not have erect leaves. Dasix, another susceptible variety, was almost intermediate and showed much variation between plants. Other varieties were observed which had erect leaves but only an intermediate degree of lodging resistance.

The data indicated that oat varieties have a characteristic erectness of leaf. Although lodging resistant varieties seemed to have very erect leaves, exceptions were not uncommon, notably Acton. While most susceptible varieties had non-erect leaves, those of Dasix were quite erect. In oats, this character did not seem to be a reliable one for differentiating lodging resistant types.

GREENHOUSE TESTS

Under greenhouse conditions, varieties exhibited differences in growth habit which were indicative of their lodging performance in the field. The culms of varieties having a high degree of lodging resistance remained upright without artificial support for a longer period than did those of very susceptible varieties. However, it was difficult to differentiate between varieties having intermediate resistance. It seems that greenhouse tests must be conducted at cool temperatures; otherwise elongation of the crown internodes causes spindly crowns and poor anchorage in nearly all varieties. A compact and well rooted crown formed below the soil level appeared to be essential if culms were to remain erect. Even under cool greenhouse conditions (approximately 40° F.) the crowns of susceptible oat varieties developed at higher levels than those of resistant varieties.

Differences in root and culm growth were easily observable but variability between plants was much greater than in field tests. It was concluded that, unless a suitable greenhouse technique can be devised, it is much better to select for lodging resistance in field grown tests.

DISCUSSION

Oat varieties with varying degrees of lodging resistance differed extensively in culm, crown and coronal root development when grown in field tests under a wide range of environmental conditions. This was exemplified by lodging resistant varieties having larger culms and a better type of root anchorage than susceptible varieties. Both characters seemed to be associated with the ability of the culms to resist bending at the ground level. Plant height also influences the degree of lodging. It was possible to formulate a lodging index based upon the combined effect of basal culm diameter, root type and height and thus to separate lodging susceptible varieties from resistant ones.

The coronal root systems were classified on a scale of 1-10. The scale was based upon differences in the size and spread of roots and in the diameter of the basal culm internodes. Plants grown in plots seeded at approximately 1 bushel per acre and at a depth of $\frac{1}{2}$-1 inch were most suitable for classification. Plants grown under widely spaced conditions were difficult to classify due to their unusual size and the large number of roots and tillers produced. The most favourable time for comparing coronal root systems was at flowering time or later. While at the end of six weeks' growth there was evidence of a sturdier plant in the resistant varieties, it was too early to adequately measure varietal differences in crowns and coronal roots.

The 8 oat varieties were studied for 3 years at 8 Experimental Stations situated from coast to coast in Canada. Under all conditions, it was possible to differentiate the lodging resistant varieties from the susceptible

ones by means of their better root development and larger culms. All lodging resistant varieties are not short nor are all susceptible varieties tall. This fact was recognized by several workers (12, 17, 34, 37). For example, the lodging resistant variety Acton is tall while the much more susceptible variety Vanguard is much shorter. However, all other factors being equal, height is important in formulating a lodging index.

The three characters, culm diameter, root type and height, were subjected to analysis by the discriminate function method and a lodging index was formed wherein the combined and relative effect of each character was expressed in one figure. By means of this index lodging resistant varieties could be distinguished from susceptible ones at all locations. The analyses showed that the order of importance of the 3 characters in contributing to lodging resistance was diameter of culm, root type and plant height. The 3 measurements are definitely affected by differences in environment from place to place and from year to year, but this was true with all varieties and comparable varietal differences remained evident.

The resistant varieties generally produced a larger number of coronal roots, particularly when grown under wide spacing. There were exceptions and since counting the number of coronal roots is a laborious process, it was not considered to be a suitable character to form part of an index. Also, since the number of coronal roots was found to be positively correlated with the diameter of the culm, all the emphasis was placed upon the latter character. It does seem natural that well anchored varieties with well developed culms, crowns and roots should also have more roots. It was observed by Hamilton (19) that oat varieties differ in the elongation and maturation of internode cells. The cells of the internodes of Dasix, one of the lodging susceptible varieties, elongated earlier and matured more rapidly than Beacon, a resistant variety. Both varieties ripen early but Beacon consistently produced more coronal roots. Possibly differences in tissue maturation affect the number of adventitious roots which a variety may produce.

Deep seeding did not affect the depth at which the crowns were formed below the soil surface but it did promote the development of a poorer root anchorage than shallow seeding. Number of tillers showed no association with lodging resistance. An inferior root type and thinner culms were the result of a 3 bushel-seeding rate as compared to a 1 bushel-rate. It appears to be quite generally recognized that heavy rates of seeding, especially on soils of good fertility, result in thin, spindly culms whose lower parts are poorly developed due to competition and shading. Also the root development of individual plants is restricted. Such plants have weak straw and poor anchorage and are unable to support the weight of the panicle during wind and rain.

Late planting tended to result in a poorer root type, especially in susceptible varieties. It has been observed that late seeded grain tended to lodge more. Also, when seeding is late, root formation may take place at higher soil temperatures. There is evidence that higher soil temperatures cause crowns to form too near the soil surface and may also cause elongation of crown internodes both of which lessen plant anchorage. Some of the factors associated with late seeding may contribute towards making the plants more susceptible to lodging.

Caffrey and Carroll (6) suggested that erectness of leaf was a decided advantage since it reduced shading and allowed better development of the basal culm regions. It is true that many lodging resistant varieties and many new resistant hybrids do have very erect leaves. Undoubtedly this does allow better culm development and such plants are able to shed water readily during wet weather. However, measurements of leaf erectness showed that all resistant oat varieties did not have erect leaves nor were those of susceptible varieties always decumbent.

Varieties showed greater differences histologically at the base of the culm, one-half inch above soil level, than were found formerly at the second internode above ground. The culm cross sections of resistant varieties were not only larger, but contained more vascular tissue and a greater area of thick walled sclerenchyma cells than culms of susceptible varieties. Most resistant types had a large number of vascular bundles. A few susceptible ones did also. It apparently does not always follow, as concluded in previous studies, that susceptible varieties have fewer bundles. Size of culm may be the more important factor to consider since number of bundles seemed to vary directly with it. Differences in the arrangement of the strengthening tissues to give maximum support to the culm may be important. It may be that if the vascular bundles and the sclerenchyma tissue are in close proximity to each other in the culm, then their strengthening effects are greater than when more widely separated. Observations indicated that in resistant varieties, the 2 strengthening tissues were closer together than in susceptible varieties. The histological differences in the basal culms, along with differences in root anchorage and height of plant, may reveal to a large extent why some varieties can resist bending and uprooting better than others.

Coronal root structure showed too much variability to be used as part of a lodging index. In corn (28), it was found that the root size tended to vary with the size of the stem. In these studies, the same tendency was evident, but there were exceptions.

Although varietal differences in root type were larger under all cultural conditions, than any particular varietal interaction, there are other conditions which affect the ratio of top to root growth and presumably have much effect on lodging. The effects of moisture, soil nutrients and leaf rust on root growth of cereals have been reported frequently. Moisture studies indicated that cereal root development varied inversely with soil water content (22, 27, 29, 33). There are considerable data to show that with oats, wheat and barley, an abundant supply of nitrogen produces a relatively smaller root system in proportion to the tops (13, 38, 41).

A high moisture supply, abundance of nitrogen, and the presence of crown rust have long been considered as aiding the conditions that bring about lodging. Since a well developed root system is considered important in lodging resistance, many of the unanswered questions regarding the effect of nutrients, moisture and disease on standing ability may become less obscure with further investigations on root development and structure.

Undoubtedly there are many factors responsible for resistance to lodging. Each may play a part in a complex relationship. The expression of each may be affected by environment and by variety. Many factors may be unknown. Some of the more important ones do seem visible and amenable to evaluation.

In breeding for lodging resistance, it appears that attention must be given to 3 characters, namely, culm diameter, root development and plant height. Lodging resistance is a varietal characteristic and its inherent nature may be associated with the above 3 characters. Several secondary factors exert a pronounced effect on the ability of a plant to remain erect during rain and wind storms. Some of these are: Rate of seeding, time of seeding, amount of disease present, fertility balance and soil type. From breeding work currently in progress it is evident that marked improvement in lodging resistance may be made by hybridizing resistant varieties and selecting well anchored plants with large culms. Better selection may be facilitated if the plants are grown where lodging is usually severe. Since large culms were found to be correlated with good root development, then many resistant types were selected by choosing plants which had large culms and moderate height although both tall and short resistant lines have been selected. In wheat (3) there is evidence that one can select for diameter of culm in early generations and that continued selections will lead to the desired type. Plants with larger culms will have larger crown internodes from which there can develop more and larger coronal roots. Possibly such plants may have more tolerance to foot rotting fungi. Large culms are likely to have more dry matter, more strengthening tissue and more of the things that a variety needs to resist lodging.

SUMMARY

1. Eight oat varieties known to differ extensively in degree of lodging resistance also differed in culm, crown and coronal root development when grown in field tests for 3 years at 8 stations which represented a wide range of environmental conditions. The plant characters investigated were considered to be those associated with lodging prior to maturity.

2. Varieties which possessed a high degree of lodging resistance also had culms of greater diameter and larger, more rigid and more widely spreading coronal root development than susceptible varieties. Culm diameter, root type and plant height were the main factors associated with lodging resistance. They were considered to be varietal characteristics whose degree of expression varied considerably between locations and years but comparable varietal differences were evident and quite consistent in all tests.

3. Coronal root systems were classified on a scale of 1-10 which was based upon differences in size and spread of roots and in the diameter of the basal culm internodes. Plants grown in plots seeded early at a rate of approximately 1 bushel per acre and at a depth of 1 inch were most suitable for classification. The best stage of growth at which to make varietal comparisons was after flowering and when the straw was still green.

4. Culm diameter was positively correlated with number of coronal roots indicating that varieties with the largest culms had the greatest number of coronal roots. Culm diameter was negatively correlated with root type indicating that varieties with the largest culms had the best root development.

5. A lodging index was designed to separate resistant from susceptible varieties. It was based upon the combined effect of basal culm diameter, root type and height. The relative importance of each character in

contributing to the index was in the order of culm diameter, root type and height. Culm diameter was considered to be an important factor as an indicator of lodging resistance.

6. A heavy rate of seeding produced an inferior root type and thinner culms. Deeper seeding tended to promote poorer root anchorage than shallow seeding. Late planting was associated with poorer root type, especially in susceptible varieties.

7. Oat varieties appear to have a characteristic erectness of leaf but the character was not found to be a reliable one for differentiating lodging resistant types.

8. Varieties showed greater histological differences at the base of the culm, one-half inch above soil level, than were found formerly at higher internodes. The culms of resistant varieties contained more vascular tissue and a greater area of thick walled sclerenchyma cells than culms of susceptible varieties. Resistant varieties did not always have the largest number of vascular bundles. The vascular bundles and the sclerenchyma tissue were in closer proximity, relative to culm diameter, in the resistant varieties thus possibly providing added strength. Coronal root anatomy was not found to be associated with lodging resistance.

9. Varietal differences in root and culm growth were easily observable in greenhouse tests but variability between plants was much greater than in field tests. There was a tendency for crowns of susceptible varieties to develop at higher levels in the soil than those of resistant varieties.

Thus, differences in development of basal culms, along with differences in root anchorage and height of plants seem to reveal to a large extent why certain varieties are able to resist bending and uprooting better than others. Large culms not only have more internal strengthening tissue but appear to be associated with better root anchorage and a more robust type of plant in general. In other words, there is evidence to show that lodging is associated with the anchorage of the plant to the ground. Resistant oat varieties appear to have sufficient anchorage to withstand the force exerted on the panicles, culms and leaves when they are being blown back and forth by the wind and particularly when the soil has been softened by rain.

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THE EFFECT OF CLIPPING FREQUENCY ON THE PRODUCTIVITY AND ROOT DEVELOPMENT OF RUSSIAN WILD RYE (*Elymus junceus* Fisch.) IN THE GREENHOUSE[1]

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INTRODUCTION

Overgrazing of pastures in dry regions is recognized as a practice which not only reduces the potential current yield, but also decreases vigour of the palatable species to such an extent that unpalatable weeds replace them and eventually may dominate the vegetation.

Russian wild rye (*Elymus junceus* Fisch.) is one of the more promising dryland pasture grasses presently being tested throughout the Canadian prairies. It was chosen for the experiment being reported, because it is desired to obtain further information relating to its growth habits. The study was undertaken to determine the effect of different intensities of utilization, simulated by clipping in the greenhouse, on the growth and vigour of the species. The information obtained may give valuable leads to future field studies that may be undertaken, and it may also help to explain the cause of the effects of certain overgrazing practices.

LITERATURE REVIEW

In a study on short-grass prairie, Clarke *et al.* (3) show that severe overgrazing brings about the decline of palatable grasses and an increase of unpalatable weeds. After seven years of overgrazing, such species as *Stipa comata* Trin. and Rupr., *Koeleria cristata* (L.) Pers., *Bouteloua gracilis* (H.B.K.) Lag., and *Agropyron Smithii* Rydb., were severely affected, being replaced by *Artemisia frigida* Willd., *Gutierrezia diversifolia* Greene, *Opuntia polyacantha* Haw., and *Phlox Hoodii* Richards, all unpalatable weeds. Lang and Barnes (9) in their studies of native grasslands found that the short season grasses *Bouteloua gracilis* (H.B.K.) Lag., and *Buchloe dactyloides* (Nutt.) Engelm. yielded more when harvested frequently than when protected to the end of the season, and showed little degeneration of ground cover. The mid-season grasses, on the other hand, were found to give the greatest yield if cut only once at the end of the season. It is suggested by the authors that the smaller yields obtained by frequent clipping may be offset by the improved quality of the forage. Weaver (17), in his studies on the effect of grazing intensity on roots, found that on a depleted range of non-vigorous grasses the roots are shallow, absorbing nutrients only near the surface, while in a vigorous stand the roots are much more extensive, penetrating the soil to greater depths. Harrison and Hodgson (6), in a greenhouse study, determined that differences existed between several grass species in the amount of injury incurred by continuous close clipping. Beginning with the one least injured, they rated the species tested in the following order: Kentucky blue grass, quack grass, smooth brome grass, timothy, and orchard grass. In nearly every case the yields of top growth and underground parts were greatest from those plants

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allowed to go unclipped. Carter and Law (2), in a recent greenhouse study with several grass species, were able to show a greatly reduced growth of all species by a 30-day as well as a 15-day clipping schedule. *Bromus inermis* was apparently injured least, while *Agropyron inerme* was almost totally eliminated from the 15-day phytometers.

Tesar and Ahlgren (14), studying the effect of height of cutting on Ladino clover (*Trifolium repens* L.), found that frequent defoliation significantly reduced the weight of live stolons and the percentage of total available carbohydrate in the stolons up to the cutting by September 10, but after this date little change occurred. The ground cover was greater under less severe clipping, and they established that four cuttings at a height of 3½ inches gave high forage yields with little invasion of grasses. Smith and Graber (12) established that the removal of top growth of sweet clover (*Melilotus alba* Desv.) in mid-September during the year of establishment markedly reduced the weight of roots. Removal of top growth earlier in the season affected sweet clover plants to a lesser degree but in a similar manner. Yields in the second year were directly correlated with the amount of carbohydrate and nitrogenous food stored in the roots during the first season before winter set in. Bär and Tseretheli (1), working on alfalfa, found that cutting during the pre-flowering period arrested root development for several weeks. This effect was not so noticeable if cuttings were made at the flowering stage or later. Seed development affected root growth in a similar manner as cutting, in that roots grew very slowly during this period. Plants cut twice during the summer when in the flowering stage went into the winter with the strongest root system. Frequent cutting greatly reduced the root growth, and the yield also was much less than from less frequent cuttings.

Under one set of conditions in Idaho, Hull (8) found that crested wheatgrass was reduced in vigour and establishment was slower when the grass was cut the first year. Hubbard (7) similarly points out that heavy grazing is detrimental to stands of crested wheatgrass the first year after seeding before plants are well established.

TABLE 1.—YIELD OF ABOVE GROUND AND ROOT MATERIAL OF RUSSIAN WILD RYE UNDER DIFFERENT INTENSITIES OF CLIPPING

Treatment	Average yield per plant in grams			
	Leaves	All above ground parts	Roots	Entire plant
A – No clipping (final cut only)	23.6	40.4	39.3	79.7
B – Clipped once at hay stage (2 cuttings)	21.7	31.5	24.6	56.1
C – Clipped at 3-week intervals (6 cuttings)	14.5	16.7	5.1	21.8
D – Clipped at 2-week intervals (9 cuttings)	9.3	10.6	2.6	13.2
E – Clipped at 1-week intervals (17 cuttings)	6.5	7.3	2.2	9.5
Least significant difference	2.1	3.2	4.8	—
Standard error per cent	5.0	5.4	11.5	—

MATERIALS AND METHODS

The Russian wild rye grass seed used in the experiment was taken from a commercial seed lot of good quality. On November 27, 1949, the seed was sown in shallow flats. Seedlings were later transplanted to 4-inch pots as single plants, and finally into 10-inch crocks where they remained until the completion of the experiment on August 22, 1950. The five clipping treatments were replicated nine times, with the plots of single plants arranged in randomized complete blocks. The plants were kept well watered throughout the entire period, care being taken to avoid water-logging of the soil. The soil used in the experiment was Haverhill clay loam (13) of good natural fertility. One part of sand was mixed with three parts of the soil to provide a suitable potting soil. Fertilizer 16-20-0 was applied at the rate of 300 pounds per acre in April just prior to the commencement of cutting treatments.

The clipping treatments applied to the grass were as follows:

A — Check, no clipping.
B — One clipping at the hay stage.
C — Clipped at three-week intervals.
D — Clipped at two-week intervals.
E — Clipped at one-week intervals.

Treatments were started on April 29 when the plants were about 8 inches high with no seed stalks having formed. The clippings were made at a height of $1\frac{1}{2}$ inches from the soil surface. At the completion of the experiment, the plants were all cut and this final yield was added to that of each respective treatment for total yield.

The per cent protein content of the total forage produced by plants on each treatment was determined on three composite samples, made up of the forage from three consecutive replicates (three plants). For treatment C, the individual clippings were analysed for protein with the object of obtaining an indication of variation in per cent protein content from one clipping to another. The protein determinations were made by the standard A.O.A.C. Kjeldahl method, with one-quarter part selenium added to the regular salt mixture. The boric acid modification of Scales and Harrison (11) was used in the distillation procedure.

At the end of the experiment, the roots plus soil were removed from the crocks. The roots were washed carefully free of soil, dried, and weighed. The crowns were removed, and their weight added to that of the above-ground material.

The roots were thoroughly pulverized, and the qualitative iodine test for starch made on one-gram samples.

To gain a measure of the reserve carbohydrates present in the roots, the extraction method of Ekelund (4) was employed. The analysis was made on one-gram composite samples from 3 replicates (3 plants), giving 3 samples per treatment. The hydrolyses of the disaccharides and more complex carbohydrates were carried out by the method of Waldron *et al.* (16), and a semi-micro quantitative determination of reducing sugars was made according to the method of Shaffer and Somogyi as modified by Underkofler *et al.* (15). The results are tabulated in milligrams of reducing sugar (available carbohydrates) per gram of root material.

FIGURE 1. Relative amount of root produced on Russian wild rye under different intensities of clipping.

RESULTS AND DISCUSSION

Yield of Vegetative Material

The yield of vegetative material separated into three parts is recorded in Table 1. The data show clearly that an increase in utilization brought about a progressively lower yield of vegetative material in Russian wild rye. The quantity of root material decreased more rapidly with an increased number of clippings than the above-ground parts, except when clipping was more frequent than every two weeks. There was no significant difference in quantity of root on the plants clipped at one- and two-week intervals. The two-week clipping interval reduced the amount of root material by 94 per cent, while the above-ground parts were decreased only by 74 per cent. These findings are practically identical with those of Carter and Law (2) where a 15-day clipping schedule gave an average reduction in root material of 92 per cent, while top production was reduced 72 per cent. Figure 1 illustrates the differences in root growth on plants as affected by the five treatments. It is quite evident that over-utilization is likely to reduce very significantly the yield in the current year. In addition, plants will be weak, unthrifty, and susceptible in winterkilling.

Protein Content of Leaves

The leaf material harvested by the five treatments contained varying amounts of protein. The per cent protein content, and the total protein yield of the leaves, are recorded in Table 2. As one would expect, the older, more mature leaves contained much less protein than the young leaves. However, it is interesting to note that there was no significant difference in the per cent protein content in leaves harvested at two- and three-week intervals, while there was a significantly higher protein content in the leaves harvested at weekly intervals.

A better picture of the nutritive value of the forage is obtained from the total protein yield. The data in the last column of Table 2 show that an interval of three weeks between clippings produced the greatest yield

TABLE 2.—PER CENT PROTEIN CONTENT OF LEAVES AND TOTAL YIELD OF PROTEIN IN LEAVES OF MATERIAL HARVESTED AT DIFFERENT INTERVALS

Treatment	Protein in leaves	Per plant protein yield in leaves
	%	Gm.
A – No clipping (final cut only)	4.20	0.99
B – Clipped once at hay stage (2 cuttings)	5.20	1.12
C – Clipped at 3-week intervals (6 cuttings)	12.53	1.82
D – Clipped at 2-week intervals (9 cuttings)	12.20	1.13
E – Clipped at 1-week intervals (17 cuttings)	13.87	0.90
Least significant difference	0.56	0.04
Standard error per cent	2.1	1.2

TABLE 3.—VARIATION OF PROTEIN CONTENT OF LEAF MATERIAL HARVESTED AT THREE-WEEK INTERVALS

Date clipped	Protein content of leaves
	%
April 29	12.84
May 20	13.58
June 10	12.97
July 1	11.98
July 22	11.58
August 12	12.28
Least significant difference	0.78
Standard error per cent	2.2

TABLE 4.—AVAILABLE CARBOHYDRATES (ROOT RESERVE) PRODUCED IN ROOTS OF RUSSIAN WILD RYE AT DIFFERENT CLIPPING INTENSITIES

Treatment	Milligram sugar per gram of root (available carbohydrates)
A – No clipping (final cut only)	9.62
B – Clipped at hay stage (2 cuttings)	8.65
C – Clipped at 3-week intervals (6 cuttings)	6.29
D – Clipped at 2-week intervals (9 cuttings)	3.13
E – Clipped at 1-week intervals (17 cuttings)	1.72

of protein. Less frequent and more frequent clipping yielded much less of this most important food material. Although only the leaves were considered in this analysis, it is quite certain that if the protein of the stem material of treatments A and B had been included the total protein yield still would have been less than that from leaves alone of three-week clippings.

Since treatment C appeared desirable from the standpoint of protein production, the leaves obtained from each clipping were analysed separately. The results are presented in Table 3. The protein content was significantly higher in the April, May, and June clippings than in the July clippings. The clipping made in August again seems to be increasing in per cent protein. The reason for the lower protein content during July may be due to the greater heat in the greenhouse during this period.

Root Reserves

The iodine test for starch gave negative results for roots from all treatments.

The analysis for available carbohydrates (a measure of root reserves) showed that very striking differences existed between the roots of plants

from the five treatments. The results of the analysis are presented in Table 4. The frequent clippings reduced the quantity of root reserve enormously. When one stops to consider that the small amount of root material produced under severe clipping (Table 1) also contains about one-fifth the amount of root reserve as the check roots, it is easily understood why heavy grazing may quickly kill out the grass in the pasture.

SUMMARY

A greenhouse study on the effect of clipping on yield, protein content, and root reserve was conducted with Russian wild rye (*Elymus junceus* Fisch.).

The total yield was progressively reduced with an increased number of clippings.

The per cent protein content of leaves was about two and one-half times as high when harvested at three-week intervals or less than when harvested at the hay stage.

The total protein yield of the leaves harvested at three-week intervals was from 60 to 100 per cent higher than that of leaves harvested at any other frequency.

The more often the grass was clipped, the less the amount of root reserve per given weight of root.

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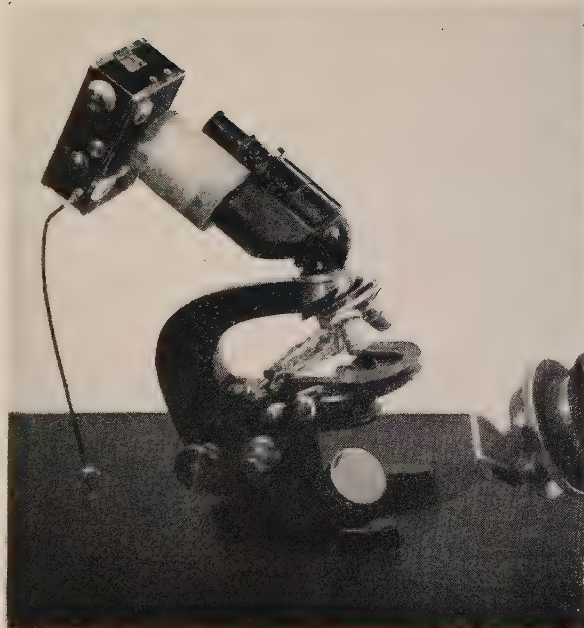

FIGURE 1. Use of ride-the-microscope mount for miniature camera.

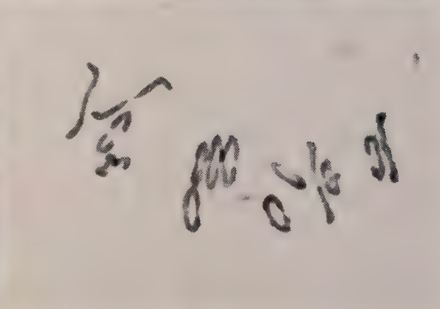

FIGURE 2 *(above)* and FIGURE 3. Mitosis and meiosis in crested wheat-grass as recorded with simplified equipment.

MINIATURE CAMERAS FOR PHOTOMICROGRAPHY[1]

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The use of ordinary hand cameras for photomicrography instead of professional equipment has been noted (1, 2, 3, 4, 5, 6). Loveland (2) has described the method in detail and indicated some disadvantages arising from the practice. The use of a 35 mm. camera for microphotography has been found reasonably satisfactory at the Dominion Forage Crops Laboratory, Saskatoon, Sask. The method is described here for the benefit of those lacking elaborate photographic equipment.

As shown in Figure 1, the miniature camera (Argus C-3) is mounted directly above the right ocular of the binocular microscope. The camera is held in place by a wooden sleeve with two inner diameters, one to fit the microscope eyepiece and the other the camera lens mounting. A reasonably tight fit is necessary to ensure that the camera is held firmly and that light is excluded. The camera also may be supported by an independent stand or post instead of using the connecting sleeve. Camera lens and eyepiece should be centred and the front surface of the camera lens should be at the eye-point of the ocular or just above (2). The camera is focused at 25 feet and the lens given the full aperture opening. Micro-file (Kodak) film with characteristics of slow speed, high contrast, and extremely good resolving power has been used.

When a field is located in the routine course of work the right eyepiece of the binocular microscope is removed, the connecting sleeve is applied and the eyepiece replaced. The camera lens mount is then inserted in the upper end of the sleeve and the camera made ready. By viewing through the left ocular the microscope is carefully adjusted for field and focus. Time exposures of 30 and 60 seconds are made in succession. Long exposures are required in view of the slow film speed and the low light intensity obtained from the standard light source. Long-exposures are not altogether undesirable as they allow some focusing for depth of field during the exposure. The use of two or more exposures is desirable because of variations in density of staining, variations in intensity of illumination, and slight errors in time and temperature of film development.

When a series of photographs is completed the film is rewound and removed from the camera. A length of film corresponding to the number of exposures taken is cut off and developed in high contrast developer (Kodak D-11). Moderate enlargement usually is required for publication. If film is purchased in bulk a fairly complete record of work can be made at low cost.

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[1] Contribution from the Division of Forage Plants, Experimental Farms Service.
[2] Agricultural Research Officer, in charge of grass breeding.

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